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# THE Festivus

Vol. 52(1)

February 2020



**Revision of the American and West African Strombidae**

**Review of *Morum* in the Western Atlantic**

**New *Neptunea* from the Eastern Bering Sea slope**

***Dolomena* strombs, fossil cowies, *Zoila*, and more**

Quarterly Publication of the San Diego Shell Club





# THE FESTIVUS

A publication of the San Diego Shell Club

Volume: 52

February 2020

ISSUE 1

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 The San Diego Shell Club, Inc.  
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*Dolomena pulchella* (Reeve, 1851) ~55 ft., fully exposed on sand. Agat Bay, Guam, 16 August 2009. Photo courtesy of Bob Abela, Guam; used with permission.  
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## MISSION STATEMENT

The San Diego Shell Club was founded in 1961 as a non-profit organization for educational and scientific purposes. More particularly to enjoy, study and promote the conservation of Mollusca and associated marine life through lectures, club meetings and field trips. Our membership is diverse and includes beginning collectors, scientists, divers, underwater photographers and dealers.

*THE FESTIVUS* is the official quarterly publication of the San Diego Shell Club, Inc. and is issued as part of membership dues in February, May, August and November. *The Festivus* publishes articles that are peer reviewed by our volunteer Scientific Peer Review Board, as well as articles of general interest to malacologists, conchologists, and shell collectors of every level. Members of the Peer Review Board are selected to review individual articles based upon their chosen field of expertise and preference. Available by request or on our website are:

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February 20, 2020 - General Meeting in Balboa Park, CA  
 March 21, 2020 - General Meeting in San Diego, CA  
 Spring Potluck & Shell Auction: 4/18/2020 from 1:00 p.m.  
 May 16, 2020 - Spring Party in Julian, CA  
 June 5 - July 5, 2020 - San Diego County Fair  
 July 18, 2020 - Shell Bazaare in San Diego, CA  
 August 21-23, 2020 - 5<sup>th</sup> Annual West Coast Shell Show

Publication date: February 1, 2020  
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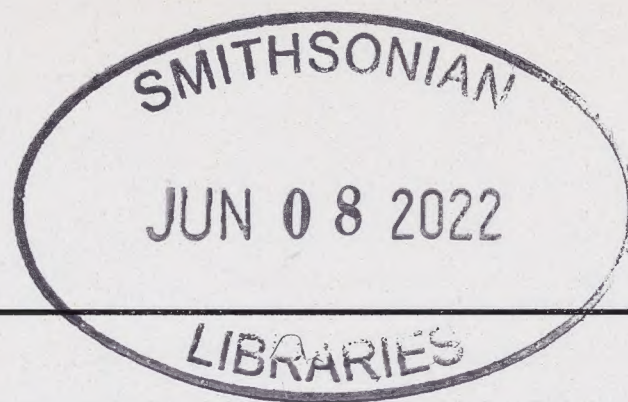


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## Towards Resolving the American and West African Strombidae (Mollusca: Gastropoda: Neostromboidae) Using Integrated Taxonomy

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**ABSTRACT** The phylogeny of the American Strombidae the genus *Lobatus* is limited to the extant *Lobatus raninus* and several fossil precursors, the genera *Macrostrombus*, *Aliger* and *Titanostrombus* are re-installed as valid genera. The genus *Persististrombus* which was used as a sink for a plethora of species, is limited to the extant *Persististrombus granulatus*, fossil American species and a few Eocene to Miocene European species, which we enclose within *Persististrombini nov. tribus* along with *Thetystrombus*. Two new genera for the Miocene ancestral basal taxa of *Aligerini nov. tribus*, *Edpetuchistrombus nov. gen.* and *Antestrombus nov. gen.*, both of which represent basal reference points enabling greater clarity in the resolution of early West African and American Strombidae radiations are proposed. This revised phylogeny informed by total evidence and historical revisions will assist in providing an evolutionary-based nomenclature that offers a structural basis for further explanation of the radiation and diversification of taxa within the Strombidae.

**KEY WORDS** Crown clade, East Africa, Strombidae, *Edpetuchistrombus*, *Antestrombus*, taxonomy, Western Atlantic

### INTRODUCTION

Higher taxonomic classifications provide a framework for the ordering of species, and with the introduction of the PhyloCode, a revolution in the way that the nomenclature is formed is coming. This paper deals with the three forms of naming that can be applied to higher taxonomic groups and applies Bryant's (1996) conventions for the defining of higher taxa. Bryant's guidelines are practically applied to the resolution of the taxonomy of West African and American Strombidae. We first examined the literature and determined relational clades for this group based on molecular and internal and external morphological relationships, and then

integrated these relationships in the standard type-based nomenclature. These relationships were contextualised with reference to ancestral relationships from the fossil record to formulate a theory of American Stromboid radiation. Associations between these clades were then defined using either stem or nodal definitions conforming to the principles of phylogenetic nomenclature. We also compared similarity-derived maximum-likelihood tree generated using combined histone 3 and cytochrome oxidase I data versus cytochrome oxidase I alone and found no difference in the level of taxonomic resolution achieved. We defined an anatomical character set which was much smaller through the removal of multiple



homeoplasies, this reduced character set had the same resolution as previous studies where those homeoplasies were included. Following construction of these trees, we mapped the published type-based taxonomy on the trees generated during the analyses to provide an insight into how alternative forms of evidence support current taxonomic understanding reflected in the nomenclature. All evidence from the relational clades and mapped taxa were considered, and a phylogeny explaining the internal relationships within the West African and American Strombidae was derived.

The West African and American Strombidae Rafinesque, 1815 have seen many taxa shuffled between genera as workers revise their understanding of morphological character relations. This rearranging of taxonomic relationships has led to cladistic instability and resulted in confusion in the nomenclature. This confusion is attributable to a major failing of modern taxonomic practice, in that it belies apomorphy-based definitions that define higher nomenclature, irrespective of the total evidence available (Latiolais *et al.* 2006; Dekkers 2008a, 2008b).

To resolve this issue and provide taxonomic clarity for the group, this review redefines the infra-familial relationships within the American and West African Strombidae Rafinesque, 1815, based on a new approach to higher taxonomic practice (Bryant 1996). In doing so, it provides a practical example of how clades are resolved and defined so as to provide a nomenclature that is stable. This stability comes with the grounding of the nomenclature in a well-resolved phylogeny and avoids the long-term problem of revisions generating paraphyletic higher taxa of older classifications (Abbott 1960, 1961; Latiolais *et al.* 2006).

We herein review the concept of clades and how they are formulated. We consider the rank of genus and subgenus as clades, as they form the first points where taxa are aggregated taxonomically. We argue that the currently accepted phylogeny of American and West African Strombidae is simplistic and is based on either a misunderstanding of the potential for reticulation among evolutionary units, or on the over-reach of generic inclusivity. These faults are grounded in a limited systematic approach that uses a purist biological concept of species but is morphologically defined in terms of criteria. This approach restricts the potential for a greater understanding in terms of a more taxonomically relevant nomenclature. We see no differentiation in the historical use of taxa at the levels of subgenera and genera for the purposes of clade recognition in this paper, as the names in use at these levels are often shuffled up and down cladistically. Therefore, we treat subgenera and genera as ranks, and application is governed by the zoological nomenclature codes on types and priority.

## THE THEORY OF HIGHER CLASSIFICATION

Higher classification in biology has two fundamental roles: it provides a practical definition for the ordering of the reference list of species, and it provides a diagnosis that describes how that list can be derived (Benton 2000). Therefore, the role of higher classification is to elucidate the evolutionary relationships between organisms and serve to provide a tool for comparative evolutionary analyses (de Queiroz and Gauthier 1990; Benton 2000). Furthermore, the diagnosis is supplemented with a description that states the innate characteristics of the organisms that are to be included within a particular rank, enabling a high level of clarity on what is, or is not, to be



included within the erected clades (de Queiroz and Gauthier 1990).

Ranks have historically been based on a need to recognise the phenotypic variability of organisms that are included under each classification and have sought to encapsulate the innate breadth and uniqueness of the characters of the organisms included (Ereshefsky 2002). Furthermore, the problem with characters is that they create ambiguity, and this leads to problems of delineation in what is naturally a continuous process of evolutionary linkage within a phylogenetic system. Hennig (1965) argued for, but later abandoned, the idea that higher taxa need to be grounded by a taxon drawn from the particular time from which the lineage arose. Furthermore, the lack of explicit time grounding avoids arguments for the need to identify the monotypic origins of higher taxa and limits the subsequent inferred nature of nodal taxa to the organisms used in its definition (Platnick 1977). Cladistic analysis needs to find the point of equivalence at which there is maximum descriptive ability and maximum explanatory power, providing the optimal delineation of a taxon (Platnick 1986).

Rank hierarchy seeks to achieve a level of positioning of a taxon relative to another that allows the creation of a class of taxa that then forms the underlying argument for ranking and subsequent ordering of the natural system (Stevens 2002). Therefore, taxa and their ancestral relationships cannot be discerned from assigned higher Linnaean ranks, which are necessary under the restrictions of that system, as they are not grounded in the phylogeny of the organisms. Linnaean ranks serve no other purpose than to group 'like' organisms. The nineteenth century concepts of adaptation, in particular the ideas of Lamarck and Darwin, were yet to be formalised when Linné formulated the system of nomenclature. This

lack of theoretical importance given to the asymmetry of ranks under the Linnaean system of nomenclature has led to the lack of evolutionary justification in tree topology and nomenclature, resulting in the assignment of higher taxa within the nomenclature that provide no insights as to the evolution of the organisms that are being classified. Therefore, there is a need for a complete restructure of the higher nomenclature (de Queiroz and Gauthier 1990, 1992, 1994; de Queiroz 1996). That is, under the Linnaean system of nomenclature, when a genus is compared to other genera, there is an implicit equality in rank, which in terms of an evolutionary grounded phylogeny, may not actually be equal.

In contrast to Linnaean nomenclature, phylogenetic nomenclature is designed to show relationships based upon a historically or evolutionary generated phylogeny. This hierarchical approach to the ordering of nature creates taxon-bearing reference points that then form the basis for relative comparisons, without any implications for the existence of ranks (Stevens 2002). Brochu and Samrall (2001) emphasize the benefit of explicitness and that universal meaning needs an explicit taxon name definition. That is, under phylogenetic nomenclature, name-bearing reference-points are used in formal definitions that are restricted by a diagnosis, thus enabling stable internal tree reconstruction (Schander 1998). This is in contrast to Linnaean nomenclature, where the assignment of taxa is singularly explicit in all definitions lacking relational explanations, thus giving rise to inherent paraphyletic problems. In contrast, phylogenetic nomenclature is fundamentally implicit. Instability in definition as a result of implicit description where relationships are given priority is only found if the definition fails to fulfil all the requirements needed to satisfy that formal definition (Benton 2000).



The use of structured or formulaic styled definitions for cladistic relationships brings clarity to the relationship between name and taxon in taxonomic definitions (Benton 2000). Much of the opposition to the acceptance of phylogenetic nomenclature is related to the misconception that it causes a loss of taxonomic freedom to deviate taxa outside the definitional framework (Lidén and Oxelman 1996; Lidén *et al.* 1997; Bryant and Cantino 2002). The disruption to the use of the nomenclature in the real world that may occur with the adoption of a phylogenetic rank-free system and the subsequent changes in nomenclature that result from different approaches to the construction of phylogenies, can be minimized if the existing type-based taxa has priority in determining the named regions of inclusivity. The use of types can avoid such instability by providing stable markers for defining the limits of inclusivity (Blackwell 2002).

Recent works that apply phylogenetic nomenclature to biological revisions have demonstrated that streamlined transitions from traditional Linnaean nomenclature to relationship-based phylogenetic nomenclature can be achieved (Cantino *et al.* 1997; Pleijel 1999; Härlin and Härlin 2001). In order to avoid ambiguity in the definition of a clade there needs to be accuracy in the wording of the definition, avoidance of reference inspecificity, and provision of phylogenetic definitions of included taxa (Bryant 1996).

### Practical Definitions in Higher Taxonomy

With the soon to be introduced PhyloCode set to revolutionize the way in which definitions are used in taxonomy, a review of the principles that govern the defining of clades needs to be explored. There are three ways a clade can be defined in higher taxa: first, node-based, where the most common ancestor of two terminals or

clades and all their descendants are included; second, stem-based, where all taxa more closely related to an organism than to another are included; and third, apomorphy-based, where all taxa that share particular unique characters are included (de Queiroz and Gauthier 1990, 1992, 1994; Bryant 1994; de Queiroz 1996; Sereno 1999; Benton 2000; Bryant and Cantino 2002).

The node-based structural definition is defined in terms of the point of delineation of two or more taxa from a common ancestor (de Queiroz and Gauthier, 1992; Sereno 1999). Any node-based definition must use taxa that are least inclusive and well nested within the clade to avoid relocation and internal inconsistency resulting in the creation of impossible clades (de Queiroz and Gauthier 1990; Schander and Thollesson 1995; Sereno 1999; Bryant and Cantino 2002). The use of names of multiple subordinate taxa in the node-based definition is only an issue in terms of stability if the taxa used in the definition are poorly supported (Sereno 1999; Bryant and Cantino 2002). All taxa that are basal need not be included. However, the definition needs to comprise enough basal taxa to avoid a more reduced inclusive clade than was originally intended. This use of designated phylogenetic context (Bryant and Cantino 2002), is a means of maximizing stability within a node-based definition. Cantino *et al.* (1997) outlined recommendations in the definition in order to maximize stability. First, there must be a level of 'substantial evidence'. Without this, there would be confusion through proliferation of phylogenetic synonyms. Second, a taxon whose membership is questionable should be avoided. Third, Sereno (1999) argued that the numbers of inclusive taxa used in the definition is dependent upon whether the clade content is well supported and nested. The use of well-supported and nested taxa will increase the



clade stability even as taxa are internally redistributed.

The stem-based structure for naming clades is based on the closer relationship between an ancestral taxon and its descendants than to more distant taxa (de Queiroz and Gauthier 1992; Sereno 1999). The stem-based definition in phylogenetic nomenclature is suited to revisions that have a lack of prior tree resolution (de Queiroz and Gauthier 1990; Sereno 1999; Bryant and Cantino 2002). The use of stem-based nomenclature also allows future division of all levels of taxa, and free movement within, or out of, a particular clade, which in turn eliminates the restrictions that the assignment of apomorphy and node-based definitions create. Dyke (2002) suggested that the movement of taxon would cause greater inclusion than the definition intended if the taxon that is used in the definition is involved in the movement. However, in his example of theropod dinosaurs, the principle concerns were of synonymic duplication as resolution increases. This is an issue for stem-based definitions only if 'proper' formulation of the principle definition from the start is lacking. Therefore, Dyke (2002) failed to recognise stability and unambiguous interpretation as having priority. It is only when priority is given to stability and clarity that the problem of proliferation of unnecessary definitions can be overcome, a concern of those who would oppose phylogenetic stem-based definitions (Dyke 2002). The stem-based definition grants higher significance to terminals, avoids ranking into unnecessary Linnaean categories, gives priority to clades, irrespective of characters and the need for inclusiveness, and is determined principally by historical phylogeny (Härlin 1999).

The apomorphy-based definition of a clade is based on the synapomorphy of the first ancestor in which it arose and includes all its descendants

(Sereno 1999; de Queiroz and Gauthier 1992). The use of apomorphy-based definitions in phylogenetic nomenclature is a major area of contention (Bryant 1994; Schander and Thollesson 1995; Pleijel 1999; Sereno 1999; Bryant and Cantino 2002). The apomorphy-based structure seeks to directly tie the actual empirical evidence to the recognition of taxa (Pleijel 1999). However, it is a fundamental concept to the study of taxonomic biology, with the focus on historicity rather than morphology that makes apomorphy-based definitions principally non-evolutionary (de Queiroz and Gauthier 1992). Bryant (1994) argued for the avoidance of apomorphy-based definitions. The restriction that this definition imposes upon the tree structure, and patterns that are absent in node and stem-based definitions, is the major fallibility in this descriptive approach. Apomorphy-based definitions are fundamentally flawed because they rely on homoplasy to allow cladistic discernment, with the actions of evolutionary processes that cause the loss of primary apomorphs, and levels of continued congruence with other apomorphs of near taxon. While Bryant and Cantino (2002) rightly point out that apomorphs do have a role in phylogenetic nomenclature, their use should be incorporated into either node or stem-based definitions as a means to give added stability.

### **BRYANT AND CROWN CLADE DEFINITIONS**

A crown taxon differs from other taxa formulations by its definition being restricted to living taxa that have an immediate extinct outgroup (Sereno 1999). While it is possible to describe a crown taxon or clade with a stem-based definition, the inadvertent use of a node-based definition is the form most widely encountered within the nomenclature (de Queiroz and Gauthier 1992; Rowe and Gauthier 1992; Wyss and Meng 1996). The use of crown



clades is common in much of the taxonomy, but this does not necessarily improve taxonomic clarity or stability unless it is accompanied by a structured definition (Lee 1996). The aim must be for the taxonomist to obtain maximum stability, and the definition of a crown clade must be determined by the state of resolution of the basal dichotomy (Sereno 1999). The use of a crown clade as a mode of definition does not preclude the recognition of ancestral taxa within it, only that these taxa are not used in the formulation of the definition. Bryant (1996) argued for eight conventions that facilitate effective phylogenetic taxonomic definitions of clades:

1. *Phylogenetic definitions should name clades identified through phylogenetic analysis.*

There needs to be an explicit phylogenetic context and pattern to the naming of a clade (de Queiroz 1994). Clades need to have a basis in evolutionary fact that supports their erection. It is unnecessary to generate ranks within a hierarchy that are “space fillers” and do not contribute to the evolutionary contextualisation of the nomenclature.

2. *Phylogenetic definitions should have standardised formats.*

There needs to be a standardised format in the naming of taxa. The use of a stem or node-based definition is the individual concern for the taxonomist and is dependent on the level of resolution of the clade under consideration (Sereno 1999). A clade that has a high level of internal resolution is more suited to the node-based definition, and is independent of outgroup relations, compared to a clade that has a low level of internal resolution, which is more suited to a stem-based definition.

3. *Typification of taxa is an optional heuristic device for standardising hierarchical relationships among clades with particular taxon names.*

It is not necessary to include a terminal taxon in the definition at every level of the hierarchy, with higher order taxonomic ranks being sufficient if inclusivity is codified (Cantino *et al.* 1997). While the use of types is redundant in phylogenetic taxonomy, as the diagnosis fulfils the role of grounding the rank in the real world, types may assist with the standardising of hierarchical relationships and in defining the most inclusive taxa (de Queiroz and Gauthier 1992; Sundberg and Pleijel 1994; Bryant 1996). Bryant (1994) argued that, for a definition to achieve accuracy, there needs to be an explicit reference to a single common ancestor in the wording. Bryant (1994) also argued that providing an ancestral basis upon which a clade is grounded needs to be with the inclusion of “most recent”, which has significant implications for the clade structure that is chosen. A clade with a poorly resolved basal relationship is best defined by a stem-based definition because the reference upon which it is founded is based on outgroups, which by definition implicitly creates the ancient ancestor. Another ambiguity in wording is created when the definition of a crown clade is dependent on the current non-extinction of members, where future extinctions would change the clade definition (Lucas 1992). This problem can be avoided if the terms ‘extant’ and ‘living’ are not used in the definition (Bryant 1994, 1996). This allows evolution of the definition and retains stability in meaning while losing extant taxa to extinction. Tautology also causes a level of ambiguity in the wording of cladistic definitions (Bryant 1996).



4. *Emendation of phylogenetic definitions is necessary in particular instances but should preserve the association between taxon names and clades.*

The need for emendation of cladistic names is often required when there is confusion in the wording of the definition and where there is a lack of clarity in meaning, or appropriateness of the taxa that are included (Bryant 1996). This is particularly relevant as the suffixes used under the codes for nomenclature that are attached to a name may not truly reflect the organizational position when contextualized with evolutionary evidence. There are no ICZN rules governing the use of prefixes, but the inclusion of "Neo+ type taxon" is advantageous to the recognition that a crown clade has been defined. This was the basis for the erection of Neostrombiodae: Prefix + type genus + suffix: Neo + Stromb + oidae for the epifamily rank.

5. *Crown clades should have "widely known taxon names".*

Where possible, existing taxonomic crown clade names should be retained in order to maintain stability. The current state of taxonomy often reflects the underlying phylogenetic understanding, albeit tied to ranks that obscure this. Therefore, a revision may involve a review and possible rejection of rules of priority in the ordering of ranks in nomenclature to save this taxonomy (Rowe 1998; de Queiroz and Gauthier 1992; Anderson 2002). This can be achieved if names are crown clades (Bryant 1996). The issue of implied ranking based on the Linnaean suffix means that the suffix should be amended to reflect the nature of the definition (convention 8 *vide infra*). Cantino *et al.* (1997) argued that current suffixes utilised by existing taxonomy could be maintained to avoid unnecessary changes and make the shift to a phylogenetic system more acceptable. In

addition, taxonomists familiar with a particular taxon would still be able to recognize the cladistic group that is implied, irrespective of the suffix.

6. *Given several "widely known taxon names" that could be used for a crown clade, the one at the lowest rank in the Linnean hierarchy should often be chosen.*

If more than one name is available within the Linnaean hierarchical system, then the lowest rank should be applied. This would leave the higher ranks available for use for more inclusive clades (Bryant 1996).

7. *Stem-based taxon names could be formed from the name of the appropriate less inclusive node-based taxon and an appropriate suffix.*

The use of a suffix should be used to indicate whether the definition is based on the node, apomorph, or stem structure. De Queiroz and Gauthier (1992) suggested *-gens* or *-genea*, and Bryant (1996) suggested *-morpha* or *-formia*. However, recent revisions make the use of these suffixes somewhat problematic due to an inconsistent application to one level of rank as internal clade structures change (Bryant 1996). Furthermore, the conflagration of stem and node names, with shifts in stem structure, may obscure the evolutionary meaning that each different approach to formulating a definition brings. In the present paper, stems are formulated in order of nomenclatural position under the ICZN (1999).

8. *Taxon names should have recommended usages.*

Bryant (1996) argues that there may be a limitation of the use of names to particular contexts, and this may reflect the level of



meaning intended at the time by the taxonomist formulating the definition. That is, there may be a need to restrict the inclusivity of a definition as the understanding of the phylogeny expands and more taxa are brought into a particular cladogram.

## TARGET TAXA AND THEIR HISTORICAL GENERIC AFFILIATIONS

We examined the taxonomy attributed to extant Strombidae Rafinesque, 1815 on the West African coast and in the Americas, and explored how the nomenclature of the subfamilies, genera, subgenera of those taxa reflects and explains the current evolutionary understanding of the relationships between those taxa. We used fossil taxa to define basal clades and to provide markers for understanding Atlantic radiations.

A list of all extant American and West African Strombidae Rafinesque, 1815 currently in general use was formulated. Each taxon was revised in order of date of description using first principles. From this list of species, their current cladistic checklist of taxa and their cladistic position was confirmed by literature review to enable a basic framework upon which to commence the revision (Table 1). Where necessary the taxonomic list was updated as the revision and higher taxonomic relationships identified were resolved and defined. All amended taxonomic positions were applied retrospectively throughout. This enabled the discussions throughout to reflect the current taxonomy and to avoid nomenclatural confusion within the text, particularly with taxa that have been moved repeatedly between genera. The checklist, therefore, represents the currently accepted living species and their generic placement (Table 1). We focused on supra-specific ranks, hence forms and subspecies were omitted. An overview of the taxonomic ranks

from subfamily to genera is presented as the systematic part of this paper.

There is a significant level of taxonomic inflation in the supra-species nomenclature. In particular, this has involved the elevation of subgenera to genera, and the displacing of the unifying genus *Strombus* Linné, 1758. We do not deal with the arguments for or against the position of infra-subtribal ranks. Rather, we treated them all based on definitional form, and they were discussed and applied appropriately and equally without rank bias. The genus and subgenus are the basal ranks, defined as the first aggregative rank in systematics.

## CURRENT TAXONOMIC RELATIONSHIPS

There have been four major systematic revisions on the nature of stromboids after Abbott (1960, 1961). Latiolais *et al.* (2006) based their work on a mix of morphology and genetics. However, the sample used was small and not representative of the diversity across the stromboid complex. Simone (2005) utilized anatomical information. However, only American and Caribbean taxa were studied. Bandel (2007) and Dekkers (2008a, 2008b) used morphology, fossil and geographical relationships, and Dekkers (2008a, 2008b) based much of his revision on the phylogeny generated by Latiolais *et al.* (2006). When these four approaches are compared, some well-defined clades are clear over all, which enable the contextualization of more focused monographs and papers within the broader clade structure (Figure 4). There have been a number of other smaller targeted monographs and papers that have contributed to understanding aspects of the cladistic relationships between West African and American taxa, and these fall into two groups: those grounded in a phenetic approach (Clench and Abbott 1941; Abbott



1960); and those that use morphology and some form of spatiotemporal evidence (Petuch 1994).

Latiolais *et al.* (2006) and Simone (2005) determined *Strombus* Linné, 1758 to contain *Strombus pugilis* Linné, 1758, *Strombus alatus* Gmelin, 1791 and *Strombus gracilior* Sowerby, 1825. Bandel (2007) combined *Strombus pugilis* Linné, 1758 with another species, *Macrostrombus costatus* (Gmelin, 1791) into the clade *Strombella* Schlüter, 1838. However, the inclusion of *Macrostrombus costatus* (Gmelin, 1791) within *Strombella* Schlüter, 1838 is problematic as it is contrary to the phylogenies presented by Simone (2005) or Latiolais *et al.* (2006) that hold for independent lineages. Clench and Abbott (1941) lumped all the Caribbean taxa within the clade *Strombus* Linné, 1758, a classification that fails to offer an explanatory reflection of the taxonomy in the nomenclature, which is a reflection on the taxonomic thinking of that time.

Latiolais *et al.* (2006) singled out *Strombus* (*s.l.*) *granulatus* (Swainson, 1822) and placed it in *Lentigo* Jousseaume, 1886. In contrast, Bandel (2007) and Dekkers (2008a) placed this taxon within *Persististrombus* Kronenberg and Lee, 2007. Similarly, *Thetystrombus latus* (Gmelin, 1791) has been shuffled with the family phylogeny during revisions, having been included in both *Lentigo* Jousseaume, 1886 (Abbott 1960) and *Persististrombus* Kronenberg and Lee, 2007 (Harzhauser and Kronenberg 2013). With the description of *Thetystrombus* Dekkers, 2008, the evolutionary understanding of the Strombidae Rafinesque, 1815 was enhanced through the provision of a West African focal point on which to base radiation theory.

The most contentious internal relationships are those within the clade identified as *Tricornis* Jousseaume, 1886 by Latiolais *et al.* (2006).

The use of this name is systematically problematic and reflects the broad lumping of species under the revisions of Abbott (1960). The genus *Tricornis* Jousseaume, 1886 (type – *Strombus tricornis* Lightfoot, 1786) currently contains two species (Bandel 2007; Dekkers 2008a), namely: *Tricornis tricornis* (Lightfoot, 1786) and *Tricornis oldi* (Emerson, 1965), considered restricted to the Indo-Pacific region (Bandel 2007).

Bandel (2007) was not so conservative in dividing up the West African-American complex, erecting three subgenera of *Strombus*: *Strombella* Schlüter, 1838 (type – *Strombus pugilis* Linné, 1758) *Mondactylus* Klein, 1753 (Type – *Strombus gallus* Linné, 1758) and *Eustrombus* Wenz, 1939 (sic = 1940) (Type – *Strombus gigas* Linné, 1758). The American stromboid taxonomy of Bandel (2007) is problematic because it does not reflect upon the cytochrome oxidase I (COI), or anatomically derived phylogenies (Latiolais *et al.* 2006; Simone 2005), which were already available, nor was it supported by Dekkers (2008a, 2008b). The use of *Aliger* Thiele, 1929 (Type – *Strombus gallus* Linné, 1758) over its junior synonym *Eustrombus* Wenz, 1940 (Type – *Strombus gigas* Linné, 1758) is correctly reflected in other revisions (Bandel 2007, Simone 2005). The use of *Lobatus* Iredale, 1921 for some members of the *Aliger* Thiele, 1929 shows a lack of understanding of the original definition of *Lobatus* Iredale, 1921 and its sister genera (Dekkers 2008b).

It is clear that the ongoing shifting of internal cladistic relationships in this complex is largely justified by the use of only a single form of evidence. The names that are applied to these clades vary, and this reflects the opinion of each taxonomist, and their understanding of what is the internal relationship, which can compound and cement taxonomic errors. These revisions



are also greatly influenced by the current state of taxonomy in the general literature, which is often grounded on smaller revisions that can overreach with the purported understanding of wider internal infra-familial relationships.

## METHODOLOGY FOR DISCERNING PHYLOGENY

Pure cladistics searches are the most parsimonious hierarchical arrangements based on character scoring of terminal taxa that do not include evolutionary considerations, nor the geographical distribution of the characters used (Davis and Nixon 1992). Thus, cladistical hierarchy is purely an epistemological axiom that is without an explanatory causal hypothesis (Brower 2000). In contrast, phylogenetics is a form of cladistics that seeks to reconstruct relationships that are dependent on the distribution of characters (Davis and Nixon 1992). In order to achieve this, species must be treated as separate terminals (Yeates 1995). In creating terminals, the taxonomist is then able to either intuitively deduce ground plan character states of the higher clades, or choose exemplars that represent real species, both of which have the same goal of providing the basis for coding (Yeates 1995). The discovery of islands of individuals within multiple most parsimonious trees enables the determination of these exemplars (Maddison 1991). Definitions should only be applied to clades after considered analysis and a sound basis for need has been established, particularly with reference to the delineation of islands out of greater diverse organism character set (Brochu and Samrall 2001). This need is systematically subjective and may be argued on a basis of phylogenetic support, phenotypic distinctiveness, ecological significance, economic importance or some other argument made by the taxonomist (Forey 2002). However, it is a phylogenetic principle that the formation of the definition of higher

taxa has stability and that there is unambiguous interpretation of what taxa are to be included and excluded. That is, uses of the name in association with a particular key stone taxon, represented by a type, must have priority (de Queiroz and Gauthier 1990).

Two forms of evidence were used to generate phylogenies for West African and American Strombidae. The cytochrome oxidase I (COI) mitochondrial subunit evidence comprised the first data set derived from Latiolais *et al.* (2006). Anatomical character states from Simone (2005) formed a second set of data. The results of this analysis were examined within the context of Bandel's (2007) and Dekkers' (2008a, 2008b) hypothetical relationships.

### *Molecular Information*

We revisited molecular data and generated new phylogenies to confirm hypothetical relationships postulated in Latiolais *et al.* (2006). Eleven COI sequences were obtained from GenBank: DQ525222 *Strombus gigas* Linné, 1758 (= *Eustrombus gigas* (Linné, 1758)) (Latiolais *et al.* 2006); DQ525223 *Strombus granulatus* Swainson, 1822 (= *Persististrombus granulatus* (Swainson, 1822)) (Latiolais *et al.* 2006); DQ525224 *Strombus latus* Gmelin, 1791 (= *Thetystrombus latus* (Gmelin, 1791)) (Latiolais *et al.* 2006); DQ525227 *Strombus peruvianus* Swainson, 1823 (= *Lobatus peruvianus* (Swainson, 1823)) (Latiolais *et al.* 2006); DQ525226 *Strombus raninus* Gmelin, 1791 (= *Lobatus raninus* (Gmelin, 1791)) (Latiolais *et al.* 2006); DQ525225 *Strombus costatus* Gmelin, 1791 (= *Macrostrombus costatus* (Gmelin, 1791)) (Latiolais *et al.* 2006); DQ525221 *Strombus gallus* Linné, 1758 (= *Aliger gallus* (Linné, 1758)) (Latiolais *et al.* 2006); DQ525220 *Strombus galeatus* Swainson, 1823 (= *Titanostrombus galeatus* (Swainson, 1823)) (Latiolais *et al.* 2006); DQ525209



*Strombus gracilior* Sowerby, 1825 (Latiolais *et al.* 2006); DQ525208 *Strombus alatus* Gmelin, 1791 (Latiolais *et al.* 2006); and DQ525207 *Strombus pugilis* Linné, 1758 (Latiolais *et al.* 2006). Sequences were aligned prior to analysis using CLUSTALW fast pairwise alignment and checked visually (Larkin *et al.* 2007). No gaps were opened in the sequences during alignment.

Molecular data were entered into MEGA X (Kumaer *et al.* 2018; Saitou and Nei 1987; Rzhetsky and Nei 1992). All trees generated were tested using 50 bootstrap replicates, the level of bootstrapping reflects the data matrix size and lack of gaps in alignment. Where multiple trees were generated, only the consensus tree is presented unless any divergence indicated a significant cladistic anomaly from another tree. Two forms of analysis were undertaken: Maximum Likelihood evolutionary history was inferred based on the Jukes-Cantor model (Jukes and Cantor 1969) and the Unweighted Pair Group Method with Arithmetic Mean (UPGMA; Sneath and Sokal, 1973), with the base assumption of a uniform rate of evolution under the Jukes-Cantor model (Nei and Kumar 2000). The ability to choose the evolutionary model overcomes many of the black box issues associated with earlier models of the MEGA software.

### Anatomical Information

Simone (2005) provided a seminal overview of the anatomy of American Strombidae Rafinesque, 1815, and the anatomical characters for eight taxa were derived from that work and used in this review: *Aliger costatus* (Gmelin, 1791) (= *Macrostrombus costatus* (Gmelin, 1791)); *Aliger gallus* (Linné, 1758); *Aliger gigas* (Linné, 1758); *Eustrombus goliath* (Schröter, 1805) (= *Titanostrombus goliath* (Schröter, 1805)); *Strombus alatus* Gmelin,

1791; *Strombus gracilior* Sowerby, 1825; *Strombus pugilis* Linné, 1758; and *Tricornis raninus* (Gmelin, 1791)(= *Lobatus raninus* (Gmelin, 1791)). Fourteen characters were utilized and coded for, and these represented differences in the anatomy of the reproductive system, buccal structure, kidneys, mantle and the organs within the cavity formed by it, and body dorsal surface textures (Table 2). Analyses of anatomical characters coded for were conducted in MEGA X (Kumaer *et al.* 2018). Trees were generated using Maximum Likelihood with a neutral evolutionary model. Character states were transcribed and coded (1 = A, 2 = G, 3 = C, 4 = T) to represent states. Maximum Likelihood evolutionary history was inferred based on the Jukes-Cantor model (Jukes and Cantor 1969). All trees generated were tested using 50 bootstrap replications, which is reflective of the data matrix size. This novel approach of using software developed for molecular analysis for character states was tested using anatomical characters against known trees that were generated with traditional software and using the same character sets and indicates no difference in internal relationships (Simone 2005).

## RESULTS

### Molecular Analyses

The maximum likelihood analysis of the COI data produced one tree with log likelihood of -3152.21 (Figure 2B). The tree generated during this retesting conformed completely to Latiolais *et al.*'s (2006) COI and H3 combined maximum likelihood gene tree (Figure 1A). The UMPGA analysis resulted in a COI gene consensus tree similar in overall branch structure and internal resolution presented by Latiolais *et al.*'s (2006) COI and Histone 3 (H3) combined maximum likelihood gene tree (Figure 2A). However, there were some differences between the two



trees. First the positioning of *Lentigo* Jousseume, 1886 (= *Persististrombus* Kronenberg and Lee, 2007; = *Thetystrombus* Dekkers, 2008) was paraphyletic in Latiolais *et al.* (2006) but is presented as the sister taxon to *Persististrombus* Kronenberg and Lee, 2007 and *Thetystrombus* Dekkers, 2008 in this analysis. Another difference is the treatment of the internal content of the Latiolais *et al.* (2006) clade *Tricornis* Jousseume, 1886 which is currently restricted to the extant Indo-Pacific. The position of *Titanostrombus* Petuch, 1994 in relation to its sister taxon remains unclear, and its position within the phylogeny is dependent on the phylogenetic methodology used (Figure 2A, B). However, results indicate a sister taxa relationship between *Macrostrombus* Petuch, 1994, *Aliger* Thiele, 1929 and *Titanostrombus* Petuch, 1994.

### Anatomical Analysis

There was no difference between the tree generated using anatomical data analysed with Mega X and that illustrated by Simone (2005) generated using more conventional cladistic programmes (cf. Figure 1B and 2C). The anatomical maximum likelihood analysis produced one tree with log likelihood of -84.77. Cladistic analysis of the anatomical evidence indicated two distinct clades. The first contained *Strombus* Linné, 1758 and this formed Simone's (2005) unidentified clade 15. The second clade, clade 16 in Simone (2005), is more complex and is represented by the *Aligerina* nov. subtribus, and is divided between: 1) *Macrostrombus* Petuch, 1994, *Lobatus* Iredale, 1921, and *Aliger* Thiele, 1929 which Simone (2005) identified as clade 18; and 2) the Simone (2005) clade 17 containing both *Titanostrombus* Petuch, 1994 and *Aliger* Thiele, 1929.

### OVERVIEW OF SYSTEMATICS

Historically, the Western Atlantic and Eastern Pacific (Panamic) stromboid species, including *Thetystrombus latus* Gmelin, 1791 from West Africa were considered monophyletic and derived from a single radiation event (Clench and Abbott 1941; Kronenberg and Vermeij 2002). Kronenberg and Lee (2007) proposed several theories to explain radiation of American stromboids. The first accepted theory is premised on the *Persististrombus* Kronenberg and Lee, 2007 arriving in one or two waves: one resulting in *Strombus* Linné, 1758 and the other accounting for all the remaining stromboids species (Kronenberg and Lee 2007). The second theory, while rejected by Kronenberg and Lee (2007), is premised on a common ancestry derived out of *Dilatilabrum* Cossmann, 1904 from the Lutetian (Middle Eocene) of Italy based on the widely extended outer lip. Purportedly, the line terminated with the Oligocene *Dilatilabrum roegli* Harzhauser, 2001. However, the placement of this taxon within *Dilatilabrum* Cossmann, 1904 needs review. The third theory also rejected by Kronenberg and Lee (2007) is grounded in Beneventi and Piccoli (1969) and Sacco (1893), where a relationship exists between American and European stromboids through the *Strombus* (s.l.) *coronatus* (Defrance, 1827) complex, which is the possible ancestor of *Thetystrombus* Dekkers, 2008. We reject all these hypotheses and argue that the radiation occurred twice at different times and from different lineages.

Furthermore, this paper addressed both the irregularities in American stromboid taxonomy. This was achieved through the use of total evidence, which brings previous revisions that used different methodological approaches together, to generate a phylogeny that illustrates the relationships between extant members of the Strombidae (Figure 3). Two clades that were



resolved here have not been identified previously, and we suggest that these represent the possible independent ancestral incursions into the Americas: *Aligerini nov. tribus* and *Persististrombini nov. tribus*. The *Persististrombini nov. tribus* includes two clades at the generic level, *Thetystrombus* Dekkers, 2008 and *Persististrombus* Kronenberg and Lee, 2007. *Thetystrombus* Dekkers, 2008 is postulated to have arisen out of a common ancestor shared with *Persististrombus* Kronenberg and Lee, 2007 (Dekkers 2008a; Harzhauser and Kronenberg 2013). This occurred during the upper Paleogene. Furthermore, the varying placement of these two clades in relation to other taxa indicates they have different evolutionary trajectories. The limitation on inclusivity within this paper makes drawing conclusions on the basal relationships between these clades problematic. This is because there is no ancestral context relative to the wider familial group outside of the defined taxa. However, the fossil records indicate a divergence between the *Persististrombini nov. tribus* and the *Aligerini nov. tribus* occurring within the upper Paleogene (Dall 1890; Petuch 2004).

Based on the distribution of the fossil records, the remaining American Strombidae Rafinesque, 1815 are not all related to *Persististrombus granulatus* Swainson, 1822, but fall into the natural clade *Aligerini nov. tribus*. Given that there is no definitively resolved outgroup to provide ancestral grounding within this study, the most appropriate definition is nodal in form. *Aligerina nov. subtribus* forms a monophyletic, enclosed and definable clade that is robustly divided into two sub-clades namely the stem clade *Strombus* Linné, 1758; and the nodal clade containing *Aligerina nov. subtribus*. These two clades represent robust clades that have evolved defining anatomical and morphological characters that enable clear delineation.

However, both share a pre-Miocene common ancestry, and we hypothesize that both are derived from a single and independent colonising event giving rise first to *Edpetuchistrombus nov. gen.* and then *Antestrombus nov. gen.* in the early Miocene of Florida.

The erection of *Aligerina nov. subtribus* represents the point of a common ancestry between *Edpetuchistrombus nov. gen.* and *Antestrombus nov. gen.*. The fossil record indicates however, that there has been a long period of divergence between these two taxa (Petuch 1994). *Lobatus* Iredale, 1921 and its *Aligerina nov. subtribus* sister crown clade share some unifying morphological characteristics, such as the tendency for distinctive uniform ribbing dorsally, the somewhat flaring lip, and the lack of sculpture within the aperture. The extant remaining members of these groups are represented by a limited number of taxa. However, each represents a greater number of fossil taxa, such that the extant taxa represent only the tip of an historical extinction iceberg. Nomenclatural significance of these taxa should not be governed only on criteria that seeks to avoid monotypicity in extant taxa. The reduction of higher taxonomic relationships based, in part, on hybridization fails to understand that successful mating can occur between genetically dissimilar organisms (Soltis and Soltis 2009). This taxonomic collapse limits the ability to construct a phylogeny that assists in explaining evolutionary theory.

The clade *Strombus* Linné, 1758 is well resolved out of the more inclusive Strombidae Rafinesque, 1815, with a diverse and rich fossil history arising out of the Miocene Lower Gatun *Edpetuchistrombus aldrichi* (Dall, 1890) complex. Practically, there is no explanatory advantage in erecting the subtribe to include



only *Strombus* Linné, 1758 as the definition of the clades is evolutionarily explicit and can be compared with taxa at any level.

*Edpetuchistrombus* nov. gen. is erected to encapsulate the lower Miocene Chipola River taxa that are directly related to *Edpetuchistrombus aldrichi* (Dall, 1890) that arrived between the Oligocene to very Early Miocene from Europe. *Strombus* (s.l.) *liocyclus* Dall, 1915, a very rare species from the Tampa Silex beds, Florida, most likely of Late Oligocene beds, is also one of the early intruders, and its placement is uncertain.

The extant *Strombus* Linné, 1758 have generally smooth body whorls except for the sometimes-strong knobs (or even spine-like knobs) and some axial growth lines. There is a general difference in form between *Edpetuchistrombus* nov. gen., which tends towards being ovate, and the biconic form of *Antestrombus* nov. gen.. *Antestrombus* nov. gen. is herein erected to encapsulate the lower Miocene (Burdigalien) Chipola River species related to *Antestrombus chipolanus* (Dall, 1890) and *Antestrombus mardieae* (Petuch, 2004). With the erection of *Edpetuchistrombus* nov. gen. and *Antestrombus* nov. gen., we hypothesise that the Miocene *Edpetuchistrombus aldrichi* (Dall, 1890) and *Antestrombus chipolanus* (Dall, 1890) complexes represent the split and transition towards *Aligerina* nov. subtribus and *Strombus* Linné, 1758. Notwithstanding, this paper argues that there were two waves, the first bringing the *Persististrombini* nov. tribus and the second wave bringing the *Tersusini* nov. tribus.

The clade *Pyramis* Röding, 1798 (Type *Strombus lucifer* Linné, 1758 = *Strombus gigas* Linné, 1758) is herein not considered taxonomically sound. The internal content of the clade indicates that Röding (1798) may have

intended this to contain juveniles of many families, that prior to reaching terminal growth, have remarkable growth similarity in shape and lip structure, and not to describe the Strombidae Rafinesque, 1815 members that are clearly placed in *Lambis* Röding, 1798.

The use of types to define basal taxa avoids paraphyletic genera as they are independent terminals of the tree. As a result of the internal resolution of the phylogeny of the American Strombidae, the genus *Lobatus* Swainson, 1837 is limited to the extant *Lobatus raninus* (Gmelin, 1791) and several fossil precursors. The genera *Macrostrombus* Wenz, 1940, *Aliger* Thiele, 1929 and *Titanostrombus* Petuch, 1994 are reinstalled as valid genera. The genus *Persististrombus* Kronenberg and Lee, 2007, which was used as a pit for a plethora of species, is now limited to the extant *Persististrombus granulatus* (Swainson, 1822), fossil American species and a few Oligocene to Miocene Indo-European species. Two new genera for the Miocene ancestral basal taxa of *Aligerini* nov. tribus, *Edpetuchistrombus* nov. gen. and *Antestrombus* nov. gen., are proposed, both of which represent basal reference points, enabling greater clarity in the resolution of early West African and American Strombidae Rafinesque, 1815.

## SYSTEMATICS

Phylum	Mollusca Linné, 1758
Superorder	Caenogastropoda Cuvier, 1797
Order	Sorbeoconcha Ponder & Lindberg, 1987
Superfamily	Stromboidea Rafinesque, 1815
Epifamily	Neostromboidae Maxwell, Dekkers, Rymer & Congdon, 2019
Family	Strombidae Rafinesque, 1815



***Persististrombini nov. tribus***

**Type.** *Persististrombus* Kronenberg and Lee, 2007 (Type: *Strombus granulatus* Swainson, 1822).

**Definition.** Contains all recent taxa of the most common ancestors shared between *Persististrombus* Kronenberg and Lee, 2007 and *Thetystrombus* Dekkers, 2008, and does not include those ancestors more closely related to *Aligerini nov. tribus*.

**Diagnosis.** A small to medium sized shell with a thin edged outer lip that may be lightly calloused in part. The outer lip is not expanded, and attaches at the shoulder of the body whorl. The sculpture of the aperture wall is variable, ranging from smooth to granulate. The columella is smooth and calloused anteriorly. The basal sinus is well developed. Shell sculpture with shoulder knobs.

**Etymology.** Formed with reference to the type genus *Persististrombus* Kronenberg and Lee, 2007.

***Persististrombus* Kronenberg & Lee, 2007**

**Type species.** *Strombus granulatus* Swainson, 1822.

**Definition.** All members more closely related to *Persististrombus granulatus* (Swainson, 1822) and the clade bound by it.

**Synonymy.** *Persististrombus* Kronenberg and Lee, 2007, p. 257

**Original Diagnosis.** “Shell of moderate size for family, fusiform, shoulder knobs distinct on body whorl, slightly expanded outer lip with sharp, unglazed rim and no extensions, regularly divided callus on columella, anterior canal short, posterior canal or groove absent or obsolete. Protoconch elongate and conical with four to five smooth whorls. Adaxial side of outer lip smooth, plicate, or granulate” (Kronenberg and Lee 2007, p. 257).

**Description.** The shell with a sharp outer lip, anteriorly strongly quadrate and not axially reflected. The inner lip is granulated or lirate. The mid-body whorl with rows of nodules. The shell is solid and heavy, with an anterior canal that is reflected.

**Assigned Taxa:** *Strombus baltrae* Garcia-Talavera, 1993 [Pliocene, Galapagos, Ecuador], *Strombus (Lentigo) barrigonensis* Jung & Heitz, 2001 [Early Pliocene, Venezuela], *Strombus granulatus* Swainson, 1821 [Pliocene to Recent, tropical eastern Pacific] (Figure 4A), *Strombus (Lentigo) insulanus* Jung & Heitz, 2001 [Middle Pliocene, Caribbean Panama], *Mitra nodosa* Borson, 1820 [Lower Miocene, Italy], *Strombus bonelli* Brongniart, 1823 [Lower Miocene, Italy], *Strombus obliterated* Hanna, 1926 [Pliocene, California, USA], *Strombus praecedens* Schaffer, 1912 [Lower Miocene, Austria], *Pterocerus radix* Brongniart, 1823 [Lower Oligocene, Italy], *Strombus (lentigo) toroensis* Jung & Heitz, 2001 [Early Pliocene, Panama].

***Thetystrombus* Dekkers, 2008**

**Type species.** *Strombus latus* Gmelin, 1791.

**Definition.** All taxa more closely related to *Thetystrombus latus* (Gmelin, 1791) and the clade bound by it, than to *Persististrombus* Kronenberg and Lee, 2007.

**Synonymy.** *Afristrombus* Bandel, 2007, p. 143 (Type: *Strombus latus* Gmelin, 1791).

**Original Diagnosis.** “Shell large to very large, solid but mostly thin walled, light to medium weight shells. The form of the shell is ovoid. Outer lip has a striking thin end which characterizes the genus. Body whorl decorated with knobs on the shoulder, sometimes nearly smooth and sometimes large to very large knobs reflecting to spines. Stromboidal notch is present, mostly large. The base left of the canal is rounded and smooth, no finger like small projections. The sculpture of the body whorl is



besides the aforementioned knobs rather smooth and consists merely of small growth line. The inside of the lip is smooth, just as the columella" (Dekkers 2008, p. 55).

**Description.** The shell with an outer lip that is centrally calloused and not axially reflected; teleoconch with regular nodulations; inner lip smooth; body whorl without striae; shell thin and light; and the anterior canal is straight.

**Assigned Taxa:** *Strombus coronatus* (Defrance, 1827) [Pliocene, Italy etc.], *Strombus exbonellii* Sacco, 1893 [Middle Miocene, Austria], *Strombus inflexus* Eichwald, 1830 [Middle Miocene, Ukraine], *Strombus lapugyensis* Sacco, 1893 [Middle Miocene, Hungary], *Strombus latus* Gmelin, 1791 [Pleistocene – Recent, Mediterranean – West Africa] (Figure 4B), *Persististrombus panonicus* Harzhauser & Kronenberg, 2013 [Middle Miocene, Austria].

### *Aligerini nov. tribus*

**Type.** *Aliger* Thiele, 1929 (Type: *Strombus gallus* Linné, 1758).

**Definition.** Contains all recent taxa of the most common ancestor between *Strombus* Linné, 1758 and *Aligerina nov. subtribus* and does not include those ancestors more closely related to *Persististrombini nov. tribus*.

**Diagnosis.** The shell is solid, heavy, with a smooth and calloused outer lip. The body whorl is smooth or with uniform axial sculpture. The basal sinus is variable in depth.

**Etymology.** Derived from the subordinate genus *Aliger* Thiele, 1929.

### *Aligerina nov. subtribus*

**Type.** *Aliger* Thiele, 1929 (Type species: *Strombus gallus* Linné, 1758).

**Definition.** Contains all members of the *Aligerini nov. tribus* that are not encapsulated within *Strombus* Linné, 1758.

**Diagnosis.** The shell is heavy and moderately large with a broad outer lip that is calloused and thickened. The basal sinus is present.

**Etymology.** Derived from the subordinate genus *Aliger* Thiele, 1929.

### *Aliger* Thiele, 1929

**Type species.** *Strombus gallus* Linné, 1758.

**Definition.** Contains all recent members of the *Aligerina nov. subtribus* that are not encapsulated within *Macrostrombus* Petuch, 1994, *Titanostrombus* Petuch, 1994 or *Lobatus* Iredale, 1921.

**Synonymy.** *Strombus (Aliger)* Thiele, 1929, p. 254; *Eustrombus* Wenz, 1940, p. 945 (Type: *Strombus gigas* Linné, 1758) [Note: A uninominal name proposed for a genus-group division of a genus, even if proposed for a secondary (or further) subdivision, is deemed to be a subgeneric name even if the division is denoted by a term such as "section" or "division"; but a name used for an aggregate of species, which is denoted by a term such as "superspecies", is not deemed to be a genus-group name (ICZN 1999, art. 6.2)]

**Original Diagnosis.** "Schale mit starken Knoten und Spiralreifen, Mundrand bedeutend erweitert und oben einen splitzen Flügel bildend" (Thiele 1929, p. 254). Shell with strong knobs and spiral ribbing, apertural rim rather broad and on the upper part winged and pointed. (Translation AMD)

**Description.** The shell outer lip is inflated, with widely, expanded, uniformly thickened lips as adults, but is not axially reflected; posterior end of lip narrowing to projection or point, giving the aperture a triangulate shape; shoulders often ornamented with large knobs; shell moderately heavy and solid; and an anterior canal that is reflected.

**Assigned Taxa:** *Strombus dominator* Pilsbry & Johnson, 1917 [upper Miocene-lower Pliocene, Dominican Republic], *Strombus galliformis*



Pilsbry & Johnson, 1917 [Pliocene, Dominican Republic], *Strombus gallus* Linné, 1758 [Pleistocene – Recent, Caribbean] (Figure 5A), *Strombus gigas* Linné, 1758 [Pleistocene–Recent, Caribbean] (Figure 5B).

### ***Lobatus* Iredale, 1921**

**Type species.** *Strombus bituberculatus* Lamarck, 1822 (= *Lobatus raninus* (Gmelin, 1791)).

**Definition.** Contains all recent members of the *Aligerina* nov. subtribus that are not encapsulated within *Macrostrombus* Petuch, 1994, *Titanostrombus* Petuch, 1994 and *Aliger* Thiele, 1929.

**Synonymy.** *Lobatus* Swainson ex Iredale, 1921, p. 208.

**Original Diagnosis.** Iredale provides a scant reference to a purported Swainson (1837) manuscript where the remark *Lobatus* is inserted next to *Strombus bituberculatus* Lamarck, 1822. “Only three names appear to be of importance: thus on p. 67, under the genus *Turbinella*, against a series beginning with *T. capitellum*, there is noted in brackets *Plicatella*, Swainson, and on p. 75, in the same manner, *Lobatus*, Swainson, is recorded for *Strombus bituberculatus*; and on p. 81. *Buccinulum*, Swainson is referred to in connection with *Buccinum lineatum*, *lineolatum*, *maculosum* and *coromandelianum*” (Iredale 1921: p.208).

**Description.** The shell is triangulate, heavy and solid; outer lip axially reflected and posteriorly tricornate with uniform callosity; mid-dorsal body whorl with striae and rows of nodules; and the anterior canal is reflected.

**Assigned Taxa:** *Strombus peruvianus* Swainson, 1823 [Pleistocene–Recent, tropical eastern Pacific] (Figure 5C), *Strombus raninus* Gmelin, 1791 [Pleistocene–Recent, Caribbean] (Figure 5D).

### ***Macrostrombus* Petuch, 1994**

**Type species.** *Strombus costatus* Gmelin, 1791.

**Definition.** Contains all recent members of the *Aligerina* nov. subtribus that are not encapsulated within *Aliger* Thiele, 1929, *Titanostrombus* Petuch, 1994 or *Lobatus* Iredale, 1921.

**Synonymy.** *Macrostrombus* Petuch, 1994, p. 258.

**Original Diagnosis.** “*Strombus* shells that are much larger than *Strombus* s.s., massive, inflated, with widely, expanded, thickened lips as adults; posterior end of lip rounded, not narrowing to projection or point; body whorls sculptured with large flattened cords, giving shells ribbed appearance; shoulders often ornamented with large spike-like knobs” (Petuch 1994: p. 258). [Comment – Petuch (1994, p. 258): “This endemic western Atlantic strombid radiation, which appears to have been centred on the Floridian Peninsula, has traditionally been placed in the subgenus *Eustrombus* Wenz, 1940 (type: *S. gigas* Linnaeus, 1758) (note: Abbott (1960) incorrectly placed *S. gigas* in *Tricornis* Jousseaume, 1886 - an unrelated, endemic Indo-Pacific, Red Sea subgenus). Since members of *Macrostrombus*, although large like *Eustrombus*, lack the large shoulder spikes of the *S. gigas* complex, have heavily-ribbed body whorl sculptures, and have more rounded, non-projecting lips, I felt it necessary to erect a separate subgenus for this compact western Atlantic group.”]

**Description.** The shell dorsum with uniform striae; teleoconch whorls knobbed; body whorl with shoulder nodulations; outer lip centrally calloused, posteriorly quadrate and thinned; outer lip edge axially reflected with glazing; aperture smooth; shell heavy and solid and an anterior canal that is reflected.

**Assigned Taxa:** *Macrostrombus bartoni* Petuch & Drolshagen, 2011 [Plio-Pleistocene,



Florida, USA], *Strombus* (*Macrostrombus*) *brachior* Petuch, 1994 [lower Pleistocene, Florida, USA], *Macrostrombus briani* Petuch & Drolshagen, 2011 [Pliocene, Florida, USA], *Macrostrombus collierensis* Petuch & Drolshagen, 2011 [Pliocene, Florida, USA], *Strombus costatus* Gmelin, 1791 [Pleistocene – Recent, Florida, Caribbean] (Figure 5E), *Strombus diegelae* Petuch, 1991 [middle Pleistocene, Florida, USA], *Macrostrombus dubari* Petuch & Drolshagen, 2011 [Pleistocene, Florida, USA], *Strombus haitensis* Sowerby, 1850 [Miocene, Dominican Republic], *Strombus* (*Eustrombus*) *hertweckorum* Petuch, 1991 [Pliocene, Florida, USA], *Strombus jonesorum* Petuch, 1994 [Pleistocene, Florida, USA], *Strombus leidy* Heilprin, 1887 [upper Pliocene, Florida, USA], *Strombus mayacensis* Tucker & Wilson, 1933 [Pliocene, Florida, USA], *Strombus* (*Macrostrombus*) *mayacensis holeylandicus* Petuch, 1994 [Pleistocene, Florida, USA], *Strombus mulepenensis* Petuch, 1994 [Pliocene, Florida, USA], *Macrostrombus oleiniki* Petuch & Drolshagen, 2011 [Pleistocene, Florida, USA], *Lobatus pascaleae* Landau, Kronenberg & Silva, 2010 [Late Miocene, Dominican Republic], *Macrostrombus sargenti* Petuch & Drolshagen, 2011 [Pleistocene, Florida, USA], *Macrostrombus tomeui* Petuch & Drolshagen, 2011 [Pleistocene, Florida, USA], *Strombus williamsi* Olsson & Petit, 1964 [Late Pliocene, Florida, USA], *Macrostrombus whicheri* Petuch & Drolshagen, 2011 [Pleistocene, Florida, USA].

### *Edpetuchistrombus* nov. gen.

**Type species.** *Strombus aldrichi* Dall, 1890.

**Definition.** Contains all ancestral members of *Aligerini* nov. tribus more closely related to *Aligerina* nov. subtribus than to *Strombus* Linné, 1758.

**Diagnosis.** Shells of moderate size; ovate; spire with spiral lines and knobs; body whorls with evenly spaced spiral ribbing that run also on the relatively large shoulder knobs; lip flaring, aperture straight, not glazed within; aperture extends posteriorly before the pre-ultimate whorl. The spiral ribbing runs over the extended lip, bending backwards. Apertural rim not glazed. The anterior canal not broad and a little reflected to the left. The Stromboid notch is present but shallow.

**Etymology.** The name *Edpetuchistrombus* nov. gen. is chosen in honour of Edward J. Petuch, Florida, USA, for the inspiring work he has done on extant and fossil molluscs in Florida and the Caribbean and especially the research on Strombidae species and genera, with his ground-breaking ideas on the seas and sub-seas and the formations from the Miocene to present.

**Assigned Taxa:** *Strombus aldrichi* Dall, 1890 [Lower Miocene, Florida, USA] (Figure 6A).

### *Titanostrombus* Petuch, 1994

**Type species.** *Strombus goliath* Schröter, 1805.

**Definition.** Contains all recent members of the *Aligerina* nov. subtribus that are not encapsulated within *Aliger* Thiele, 1929, *Macrostrombus* Petuch, 1994 or *Lobatus* Iredale, 1921.

**Synonymy.** *Titanostrombus* Petuch, 1994, p. 261.

**Original Diagnosis.** “*Strombus* shells that reach the largest sizes for the family, massive, inflated, with uniformly thin, expanded lips as adults; posterior end of lip rounded; body whorls sculptured with wide, closely-packed, flattened ribs; spire whorls low and generally flattened; spire whorls often with large spike-like knobs; knobs become obsolete on body whorl; body whorl rounded, without spikes or knobs; shoulder rounded, often with faint axial undulations” (Petuch, 1994: p. 261). [Comment – Petuch (1994, p. 261): “This group



of giant strombids is unique to the tropical Americas, with a living species in both the Eastern Pacific and western Atlantic (Brazil). The only known fossil species, *S. williamsi* (Plate 20, Figure A) is found only in the Holey Land Fauna of the Everglades region, and is known from fewer than a dozen specimens. While *S. (Titanostrombus) goliath* is the largest living species, *S. (Titanostrombus) williamsi* is the largest-known fossil strombid (with specimens in excess of 300 mm). *Titanostrombus* is similar to *Macrostrombus*, but differs in being consistently larger, in having more rounded shoulders, and in having large, spikelike knobs on the early whorls. In this last character, *Titanostrombus* is similar to *Eustrombus* (type *S. gigas*). The co-occurrence of three giant strombid genera, *Macrostrombus*, *Eustrombus*, and *Titanostrombus*, together in southern Florida during Holey Land time, is truly remarkable".]

**Description.** The shell outer lip is uniformly thin on the border, thickened centrally, expanded and rounded posteriorly; body whorl sculptured with broad narrow interspaced ribs; teleoconch often with large knobs; knobs become obsolete on body whorl; shell moderately heavy and solid; and an anterior canal that is reflected.

**Assigned Taxa:** *Titanostrombus immokaleensis* Petuch & Drolshagen, 2011 [Pliocene, Florida, USA], *Strombus galeatus* Swainson, 1823 [Pleistocene – Recent, tropical East Pacific] (Figure 5F), *Strombus goliath* Schröter, 1805 [Recent, Brazil] (Figure 5G).

### *Strombina nov. subtribus*

**Type.** *Strombus* Linné, 1758 (*Strombus pugilis* Linné, 1758 by subsequent designation Lamarck (1799)).

**Definition.** Contains all recent members of the *Aligerini nov. tribus* that are not encapsulated within *Aligerina nov. subtribus*.

**Diagnosis.** Shells biconic with the apertural rim not glazed. The edge of lip somewhat thickened posteriorly and calloused, becoming thinner and sharper anteriorly.

**Etymology.** Derived from subordinate genus *Strombus* Linné, 1758.

### *Antestrombus nov. gen.*

**Type species.** *Strombus chipolanus* Dall, 1890.

**Definition.** Contains all ancestral members of the clade *Strombini nov. tribus* more closely related to *Strombus* Linné, 1758 than to *Aligerina nov. subtribus*.

**Diagnosis.** Shells of moderate size. Spire acute, with spiral lines and axially aligned knobs. Body whorl reversed conoidal form. The body whorl has evenly spaced spiral ribbing that is almost smooth, with relatively large and sharp shoulder knobs. The non-flaring lip with a straight side. The aperture large but narrow and not extending posteriorly before the body whorl. The spiral ribbing runs over the extended lip and bends slightly backwards at the posterior end. The apertural rim not glazed but a little thickened by shell material added from the inside of the aperture. Inside outer lip smooth. The anterior canal not broad, but deep, and slightly reflected to the left. Stromboid notch present but shallow.

**Etymology.** The name *Antestrombus nov. gen.* is chosen to indicate the close resemblance with fossil and extant species of the genus *Strombus* Linné, 1758. The prefix *ante* is indicative that species belonging to the new genus are precursors of a plethora of species that evolved and thrived in the Plio-Pleistocene of Florida and the Caribbean Seas.

**Assigned Taxa:** *Strombus chipolanus* Dall, 1890 [lower Miocene, Florida, USA] (Figure 6 B), *Strombus dodoneus* Gardner, 1947 [Late Miocene, Florida, USA], *Strombus mardieae* Petuch, 2004 [lower Miocene, Florida, USA] (Figure 6 C). Note: *Strombus dodaneus* Gardner,



1947 is bridging between *Antestrombus* nov. gen. and *Strombus* Linné, 1758.

### ***Strombus* Linné, 1758**

**Type species.** *Strombus pugilis* Linné, 1758 by subsequent designation Lamarck (1799).

**Definition.** Contains all recent members of the *Aligerini* nov. tribus that are not encapsulated within subtribe *Aligerina* nov. subtribus.

#### **Synonymy.**

*Strombus* Linné, 1758, p. 742;

*Strombella* Schlüter, 1838, p. 22 (Type: *Strombus pugilis* Linné, 1758);

*Pyramis* Röding, 1798 (Type: *Pyramis striata* Röding, 1798 = *Strombus pugilis* Linné, 1758).

**Description.** The shell triangulate to fusiform, medium in size, The columella smooth, and the outer-lip strongly axially quadrate posteriorly. The edge of the lip somewhat thickened posteriorly and calloused, becoming thinner and sharper anteriorly. The shoulder with nodules, and the body whorl is smooth or with fine axial uniform striations. The outer aperture smooth, or with fine short lirations.

**Assigned Taxa:** *Strombus acanthospira* Landau, Kronenberg, Herbert & Silva, 2011 [Calabrian: Pleistocene, Panama], *Strombus alatus* Gmelin, 1791 [Pleistocene - Recent, Florida & Caribbean] (Figure C), *Strombus arayaensis* Landau and Silva, 2010 [Pleistocene, Venezuela], *Strombus ayersensis* Petuch & Drolshagen, 2011 [Pleistocene, Florida, USA], *Strombus bifrons* Sowerby, 1850 [Late Miocene, Dominican Republic], *Strombus capelettii* Petuch, 1994 [Middle Pleistocene, Florida, USA], *Strombus cannoni* Petuch & Drolshagen, 2011 [Pliocene, USA], *Strombus elegantissimus* Landau, Kronenberg, Herbert & Silva, 2011 [Late Pliocene, Panama], *Strombus erici* Petuch, 1994 [Calabrian Pleistocene, USA], *Strombus evergladesensis* Petuch, 1991 [Pleistocene, USA], *Strombus floridanus* Mansfield, 1930

[Upper Miocene, USA], *Strombus gatunensis* Toula, 1909 [Miocene, Panama], *Strombus gracilior* Sowerby, 1825 [Recent, Eastern Pacific] (Figure 4D), *Strombus jenniferae* Petuch & Drolshagen, 2011 [Pleistocene, USA], *Strombus keatonorum* Petuch, 1994 [Lower Pleistocene, Florida, USA], *Strombus leurus* Woodring, 1928 [Pliocene, Jamaica], *Strombus lindae* Petuch, 1991 [Pleistocene, USA], *Strombus propegracilior* Dall & Ochsner, 1928 [Pliocene, Galapagos], *Strombus proximus* Sowerby, 1850 [Miocene, Dominican Republic], *Strombus pugilis* Linné, 1758 [Recent, Caribbean] (Figure 4E). *Strombus pugiloides* Guppy, 1873 [Pliocene, Jamaica], *Strombus sarasotaensis* Petuch, 1994 [Pliocene, USA], *Strombus subgracilior* Durham, 1950 [Middle and Upper Pliocene], *Strombus vermeiji* Landau, Kronenberg, Herbert & Silva, 2011 [Neogene, Panama], *Strombus worki* Petuch, 1983 [Recent, Brazil] (Figure 4F).

### **DISCUSSION**

One of the most significant problems in bringing an evolutionary understanding to the nomenclature is the blurring of ancestral relationships through overreach within the census literature in attribution to *Persististrombus* Kronenberg and Lee, 2007. The blurring of ancestral relationships through the oversimplification of the higher taxonomy has decreased the contribution that these genera can make to the evolutionary understanding of taxonomic radiations on a global scale (Dekkers 2008b). Lozouet and Meaestrati (1986) demonstrated the link between the European Early Oligocene *Persististrombus radix* (Brongniart, 1823) (France, Aquitaine Basin) and the extant *Persististrombus granulatus* (Swainson, 1822). The overreach of the consensus in definable inclusivity within *Persististrombus* Kronenberg and Lee, 2007 has had the negative side effect of creating a level of



taxonomic inflation, where the increase in attributed taxa with more diverse morphology indirectly expands the accepted character set, and where the importance of the inclusivity within the genus appears to override the original description. The genus *Persististrombus* Kronenberg and Lee, 2007 is herein restricted to the American species: *P. granulatus* (Swainson 1822), *P. barrigonensis* (Jung and Heitz, 2001), *P. toroensis* (Jung and Heitz, 2001), *P. insulanus* (Jung and Heitz, 2001), *P. obliterated* (Hanna, 1926) and *P. baltrae* (Garcia-Talavera, 1993). Kronenberg and Lee (2007) included ancestral species that fall outside the defining characteristics of that clade *Persististrombus* Kronenberg and Lee, 2007, such as *Edpetuchistrombus aldrichi* (Dall, 1890), *Antestrombus mardiae* (Petuch, 2004) and *Antestrombus chipolanus* (Dall, 1890).

*Thetystrombus* Dekkers, 2008 is found only in the tropical part of West Africa, with records indicating that *Thetystrombus latus* (Gmelin, 1791) entered the Mediterranean basin during a relatively short period of warming in the Pleistocene (Taviani 2014). The evidence in the form of *Thetystrombus coronatus* (Defrance, 1827) places this genus from as early as the Pliocene of Spain and Italy. There is a high degree of phenotypic plasticity in the recent shells of *Thetystrombus latus* (Gmelin, 1791) ranging from slender smooth shells without shoulder knobs to large and broad shells with strong shoulder knobs. Fossil Mediterranean examples clustered within *Thetystrombus bubonius* (Lamarck, 1822), a probable synonym of *Thetystrombus latus* (Gmelin, 1791). *Thetystrombus coronatus* (Defrance, 1827) from the Pliocene of Spain and Italy represents the ancestral Mediterranean species, however, lacks the variability in morphology commonly observed in modern *Thetystrombus* Dekkers, 2008 taxa.

*Strombus* Linné, 1758 have generally rather smooth shells with more or less strong spines on the shoulder of the body whorl and the spire whorls, and a smooth inside of the outer lip. They are confined to the tropics of the Caribbean and the East Pacific coastline from northern Peru to Mexico. *Strombus* Linné, 1758 arose in the late Miocene/Early Pliocene most likely sharing a common ancestry with a Miocene member of *Antestrombus* nov. gen. Species of *Strombus* Linné, 1758 show remarkable differences in shell form and shoulder knobs (or spines) in time and space. The genus shows remarkable adaptability demonstrated by rapid radiation and shift in morphological form (Petuch 2004).

*Lobatus* Iredale, 1921 is limited to two extant species: *Lobatus raninus* (Gmelin, 1791) and *Lobatus peruvianus* (Swainson, 1823) (Kronenberg and Lee 2007; Landau *et al.* 2008). The modern re-introduction of *Lobatus* Iredale, 1921 (Petuch 1994) was contested (Jung and Heitz 2001), but later restabilised (Kronenberg and Lee 2007), and there has been a level of taxonomic overreach with the problematic collapse of *Macrostrombus* Petuch, 1994, *Titanostrombus* Petuch, 1994 and *Aliger* Thiele, 1929 into *Lobatus* Iredale, 1921 (Freiheit and Geary 2009), which we reject. *Strombus* (Lentigo) *fetus* Jung and Heitz, 2001 and *Strombus* (s.l.) *dominator* Pilsbry and Johnson, 1917 are designated here as *Lobatus* Iredale, 1921 species. “*Lobatus*” first appeared in 1837 in an anonymous catalogue of the Manchester museum where Swainson was working on the collection.

Based also on classical Swainson spelling errors, Iredale (1921) attributed the work to him; however, this cannot be verified. Therefore, according to ICZN (1999) article 14, anonymous authorship before 1951 does not prevent availability of a new name or



nomenclatural act. The anonymous work attributed to Swainson was a simple catalogue listing shells in the collection of the Manchester Natural Museum and elucidated upon first by Iredale (1921). Iredale (1921) accepted *Lobatus* as an available name drawn for the anonymous booklet, and confirmed the type as *Strombus bituberculatus* Lamarck, 1822 (= *Lobatus raninus* Gmelin, 1791). Consequently, Iredale (1921) offered the formal name and defined the taxa and takes authorship.

The genus *Macrostrombus* Petuch, 1994 was introduced as a new subgenus (the *modus operandi* at that time) with the type species being the extant *Macrostrombus costatus* (Gmelin, 1791). This large species with a rounded flaring lip, coarse spiral ribbing, and lacking large shoulder spike is an endemic West Atlantic radiation with numerous species, especially in the Plio-Pleistocene of the Florida fossil beds. Approximately 20 were described by Petuch (1991, 1994; Cf. Petuch and Drolshagen 2011) with the main focus around Florida, which was part of the Caloosahatchian Province, where Petuch (1982) proposed a centre of radiation. *Macrostrombus haitensis* Sowerby, 1850 from the Lower Gatun is the earliest known member of the clade in the Americas. Diversification within *Macrostrombus* Petuch, 1994 was primarily during the Middle Gatun. *Edpetuchistrombus* nov. gen. from the Miocene of Florida is seen as the immediate ancestral clade to the crown clade *Macrostrombus* Petuch, 1994. *Macrostrombus haitensis* (Sowerby, 1850) is bridging between *Edpetuchistrombus* nov. gen. and *Macrostrombus* Petuch, 1994, but the general characters of the shells (larger size, more reflected outer lip, glazed rim) shows it belongs to *Macrostrombus*.

*Titanostrombus* Petuch, 1994 arose in the Middle Gatun and holds the largest stromboid

species in the American radiations. The two attributable species to *Titanostrombus* Petuch, 1994, one each side of the Panama Isthmus, indicate a shared common ancestor from at the latest 3 million years ago. The shifting taxonomic placement of *Titanostrombus galeatus* (Swainson, 1823) under differing modalities may be reflective of the potential for rapid divergence, given the significant impacts of historical sea level oscillations on the narrow habit range potential for West American coastal marine species. The analysis of the provinces, and the splitting in two separate Miocene to Pleistocene Pacific-Caribbean provinces before the closure of the Isthmus, is important to understand the connection between the two gigantic stromboid species that are descendants of the southern Gatunian Province of Petuch (2004). The extant Brazilian *Titanostrombus goliath* (Schröter, 1905) and *Titanostrombus galeatus* (Swainson, 1823) from the Panamic Province, Eastern Pacific tropical coasts, are both survivors that were parted by the closure of the Central American Seaway. This *Titanostrombus* Petuch, 1994 lineage was confined to the southern part of the Pacific-Caribbean Miocene-Early Pleistocene Sea centred on Florida (Woodring 1959, 1966, 1974).

### Further Research

This review did not consider the relationships between the early Indo-Pacific and the American taxa, primarily due to the lack of detailed distributional and stratigraphic knowledge and resolution in the Indo-Pacific fossil taxa. Notwithstanding, the level of convergence in shell morphology in the fossil record between American and Indo-Pacific taxa presents an avenue for global perspectives of Strombidae radiation theory to be developed. Examples of this convergence include: *Tricornis maximus* (Martin, 1883) and *Aliger*



*gigas* (Linné, 1758), and *Tricornis tuberosus* (Martin, 1883; Indonesian Miocene) and *Macrostrombus costatus* (Gmelin, 1971). These similarities were also noted by Abbott (1960, p. 62), particularly with relation to *Tricornis tuberosus* (Martin, 1883): “I know of no recent Indo-Pacific species resembling it, although *Strombus costatus* Gmelin, 1971 of the West Indies is somewhat similar.”

## CONCLUSION

We proposed that the American Tersusini *nov. tribus* and *Strombus* Linné, 1758 are derived from a common ancestor that arrived into the Americas well before the Miocene, probably from the European Tethys. Furthermore, we argue that the ancestor of *Persististrombus* Kronenberg and Lee, 2007 arrived in the Americas prior to the closure of the Panama Isthmus, and also prior to the arrival of the ancestral lines of the Tersusini *nov. tribus*. The clades erected here are primarily monotypic in terms of extant taxa, and the fossil taxa are mostly well attributable. Similar to an iceberg, the extant taxa represent only a small portion of the taxa encompassed with the definition, while the bulk of taxa are fossils that are unseen or ignored by many extant-focused researchers. The importance of these monotypically extant clades as markers in the understating of the entire evolution and radiation of the West African and American Strombidae is through the establishment of nomenclatural reference points that enable phylogenetic explanations, without falling into the pitfalls of inclusivity debates regarding the content of the clade. Furthermore, failing to recognize iceberging with genera with limited extant taxa, and understanding the role that genera play in enabling the recognition of discrete and evolutionary progression is one of the major failings of the historical revisions into Strombidae, where the focus has been bogged at

the interspecies level without resolution. The use of phylogenetic nomenclature, and stem and nodal definitions give a level of stability in definition to the hypothesized phylogeny that has been lacking in previous attempts to resolve the West African and American Strombidae Rafinesque, 1815. Clench and Abbott (1941) applied a fundamentalist biological concept of species to their revision of American stromboids, and this is reflected in their approach to taxonomic practice. That is, the propensity for the crown clades to throw up inter-clade hybrids led to the conceptualization of closeness in relation, and therefore species were classified and aggregated in that light. This rigid adherence to a specific species concept reflects the breaking of the phenetic dominance of the past two centuries. However, one of the natural consequences was the over simplification through synonymization of many taxonomic groups. We demonstrate that a greater resolution can be achieved with a level of conceptional flexibility and a pluralist approach to the definition of taxonomic entities. The new definition explicitly defines the level of inclusivity, and places that taxonomic entity within a nomenclature that is founded on an evolutionary framework. We suggest that over simplification of higher clades based on a singular conceptualization is poor systematic practice.

## ACKNOWLEDGEMENTS

We thank Edward Petuch, Florida, USA, for the inspiration for us to study the American stromboid radiations. Also, we thank A.J.F. Janssen, Bovenkarspel, of the Netherlands for the help in getting literature written by Edward Petuch. The second author wishes to thank Henk Dekker, Winkel, of the Netherlands, for sharing ideas and opinions on the evolution and radiations of stromboid genera and species. A special mention goes to Trevor and Marguerite



Young of Cannonvale, Queensland whose invaluable assistance was gratefully accepted in the editing of this manuscript.

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Extant Taxa	Accepted Generic Affiliation (Base Clade)	Alternative Generic Affiliations
<i>alatus</i> Gmelin, 1791 <i>pugilis</i> Linné, 1758 <i>gracilior</i> Sowerby, 1825 <i>worki</i> Petuch, 1983	<i>Strombus</i> Linné, 1758 – Lamarck 1799; Montfort 1810; Clench and Abbott 1941; Abbott 1960; Latiolais <i>et al.</i> 2006	<i>Lambis</i> – Röding 1798 <i>Strombella</i> – Schlüter 1838; Bandel 2007
<i>costatus</i> Gmelin, 1791	<i>Macrostrombus</i> Petuch, 1994	<i>Aliger</i> – Dekkers 2008b <i>Strombella</i> – Bandel 2007 <i>Strombus</i> – Gmelin 1791; Clench and Abbott 1941 <i>Tricornis</i> – Abbott 1960; Latiolais 2006
<i>gallus</i> Linné, 1758  <i>gigas</i> Linné, 1758	<i>Aliger</i> Thiele, 1929 – Dekkers 2008b	<i>Aliger</i> – Dekkers 2008b <i>Eustrombus</i> – Dekkers 2008b <i>Strombus</i> – Linné 1758; Gmelin 1791; Clench and Abbott 1941 <i>Tricornis</i> – Abbott 1960; Latiolais 2006
<i>goliath</i> Schröter, 1805  <i>galeatus</i> Swainson, 1823	<i>Titanostrombus</i> Petuch, 1994	<i>Aliger</i> – Dekkers 2008b <i>Eustrombus</i> – Dekkers 2008b <i>Strombus</i> – Clench and Abbott 1941 <i>Tricornis</i> – Abbott 1960; Latiolais 2006
<i>peruvianus</i> Swainson, 1823  <i>raninus</i> Gmelin, 1791	<i>Lobatus</i> – Iredale, 1921	<i>Aliger</i> – Dekkers 2008b <i>Lobatus</i> – Dekkers 2008b <i>Strombus</i> – Gmelin 1791; Clench and Abbott 1941 <i>Tricornis</i> – Abbott 1960; Latiolais 2006
<i>granulatus</i> Swainson, 1822	<i>Persistristrombus</i> Kronenberg and Lee, 2007 – Dekkers 2008b; Harzhauser & Kronenberg 2013	<i>Lentigo</i> – Abbott 1960; Latiolais 2006
<i>latus</i> Gmelin, 1791	<i>Thetystrombus</i> Dekkers 2008	<i>Afristrombus</i> Bandel, 2007 <i>Lentigo</i> – Abbott 1960 <i>Persistristrombus</i> – Harzhauser and Kronenberg 2013 <i>Strombus</i> – Gmelin 1791

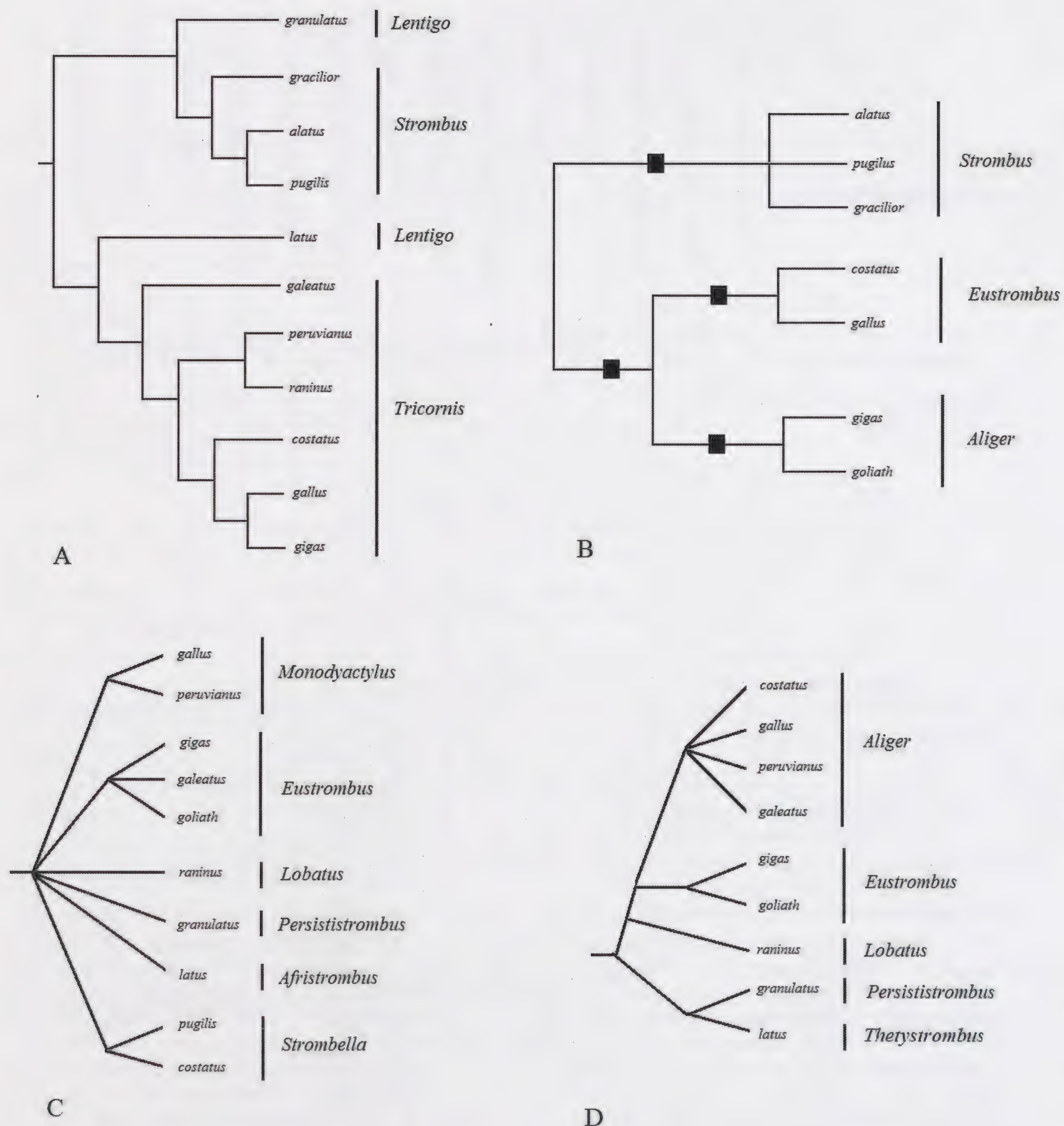
**Table 1.** The extant American and West African Strombidae taxa with the accepted and alternative generic affiliations that have been applied to those taxa.



Anatomical Character	Mouth- anterior margin	Foot - dorsal surface texture	Diaphragmal septal muscle	Operculum spines	Mantle margin	Osphradium posterior extremity	Osphradium central region	Kidney lobes	Buccal mass muscle 3 pair	Verge distal appendage	Verge dorsal longitudinal lobe	Oviduct closure	Egg Capsule gland	Seminal receptacle
Simone (2005) code	8	20	21	26	28	33	34	51	63	90	91	93	94	96
<i>alatus</i>	1	0	0	1	0	0	0	1	0	0	1	1	1	0
<i>costatus</i>	0	1	0	1	1	0	1	0	1	2	1	1	1	1
<i>gallus</i>	0	1	0	1	1	0	1	0	1	2	1	0	1	0
<i>gigas</i>	0	1	1	0	0	0	0	0	1	1	1	1	1	0
<i>goliath</i>	0	1	1	0	0	0	0	0	1	1	1	1	0	0
<i>gracilior</i>	1	0	0	1	0	0	0	1	0	0	1	1	0	0
<i>pugilis</i>	1	0	0	1	0	1	0	1	0	0	1	1	1	0
<i>raninus</i>	0	1	0	1	1	0	1	0	1	3	0	1	0	0
Simone (2005) coding states: 8 – 0 = Smooth, 1 = Papillate; 20 – 0 = Smooth, 1 = Reticulate; 21 – 0 = Present, 1 = Double layered; 26 – 0 = No spines, 1 = With spines; 28 – 0 = Smooth, 1 = Anterior tentacle; 33 – 0 = Anterior of gill, 1 = At gill level; 34 – 0 = Simple weakly curved, 1 = Sigmoid region; 51 – 0 = Similar size, 1 = Single ventral lobe; 63 – 0 = United with each other anterior to the radula nucleus, 1 = Inserted into the radula nucleus; 90 – 0 = Flat with longitudinal appendage, 1 = Semi-circular with central undulating folds; 2 = With a pair of while papillated folds; 3 = Long and massive papilla some distance from the tip; 91 – 0 = Absent, 1 = With apical projection; 93 – 0 = Entirely open, 1 = Partially opened; 94 – 0 = Separate from oviduct, 1 = Secondary expansion of the oviduct; 96 – 0 = Without folded dorsal wall, 1 = With folded dorsal wall.														

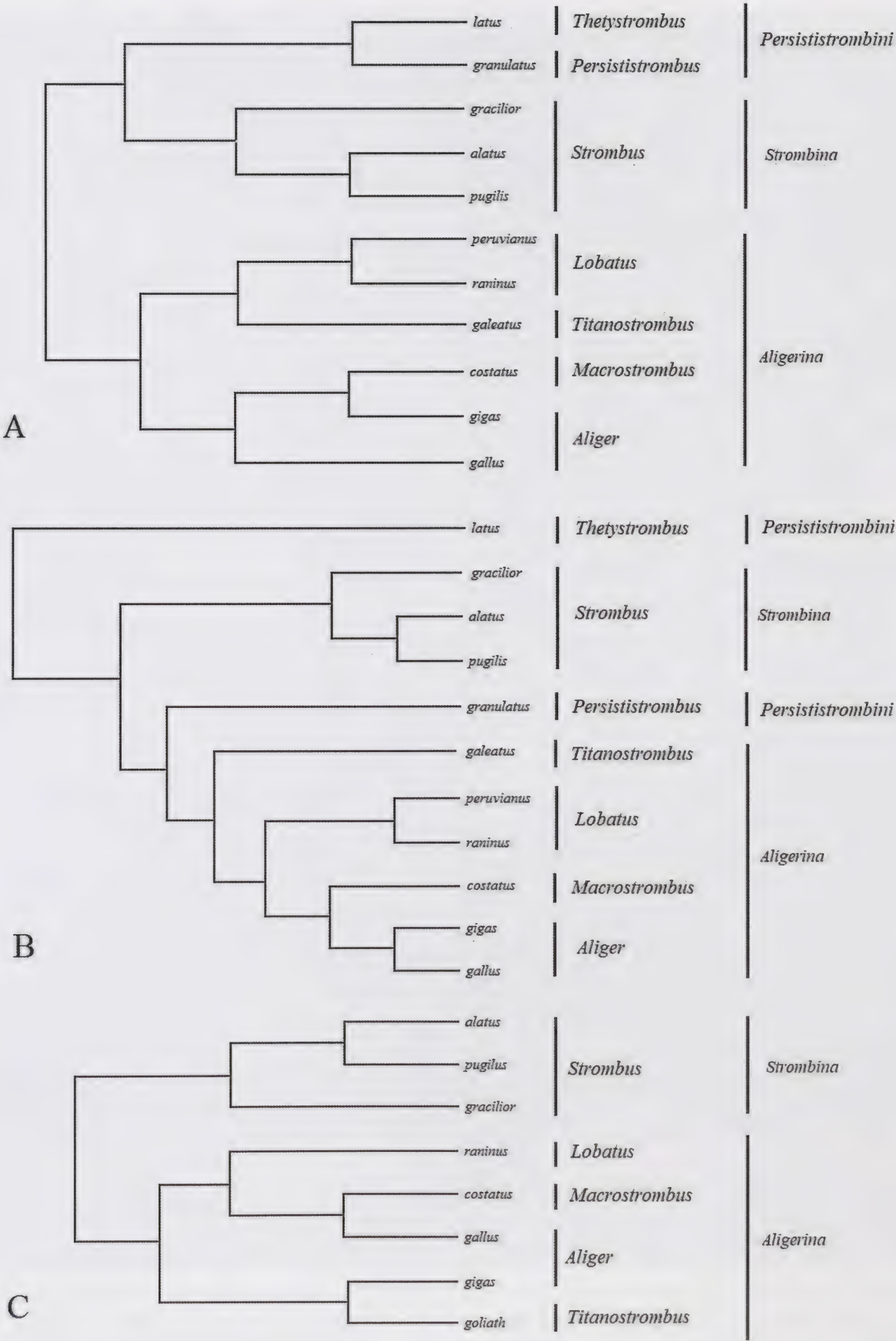
**Table 2.** The table of comparative anatomy for members of the American Strombidae.





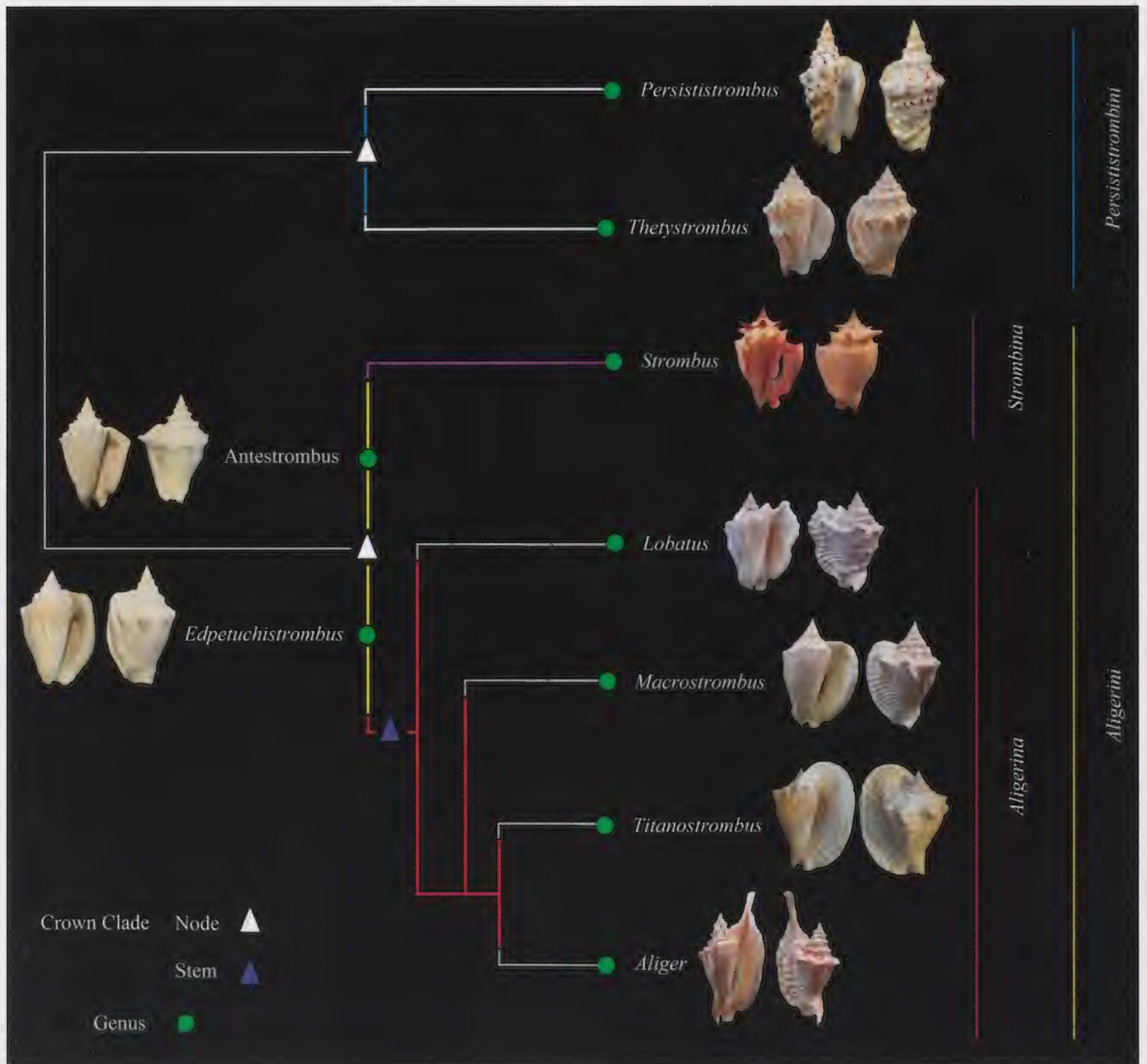
**Figure 1.** The hypothesised phylogenies of extant West African and American Strombidae and the hypothesized cladistic arrangements presented by each taxonomist: A) after Latiolais *et al.* (2006) maximum likelihood gene tree generated using combined COI and H3 molecular data; B) after Simone (2005) cladistic tree showing the anatomical relationships and significant taxonomic stem points identified by that author; C) inferred tree after Bandel (2007) based on the morphological and fossil relationships defined within the work; and D) the inferred tree after Dekkers (2008a, 2008) literary evidence, morphological, fossil and geographical relationships outlined within that work.





**Figure 2.** The morphological and anatomical cladistic trees: A) The tree generated to show similarity using COI molecular data analysis using maximum likelihood, set to zero branch collapse; B) The consensus tree generated to show hypothesized evolutionary relationships based on COI molecular data UMPGA; and C) The tree generated to show similarity using anatomical data analysis using maximum likelihood.





**Figure 3.** Hypothesized internal resolution of the American and West African genera of Strombidae based on anatomical, morphological and molecular evidence contextualized with the fossil record.





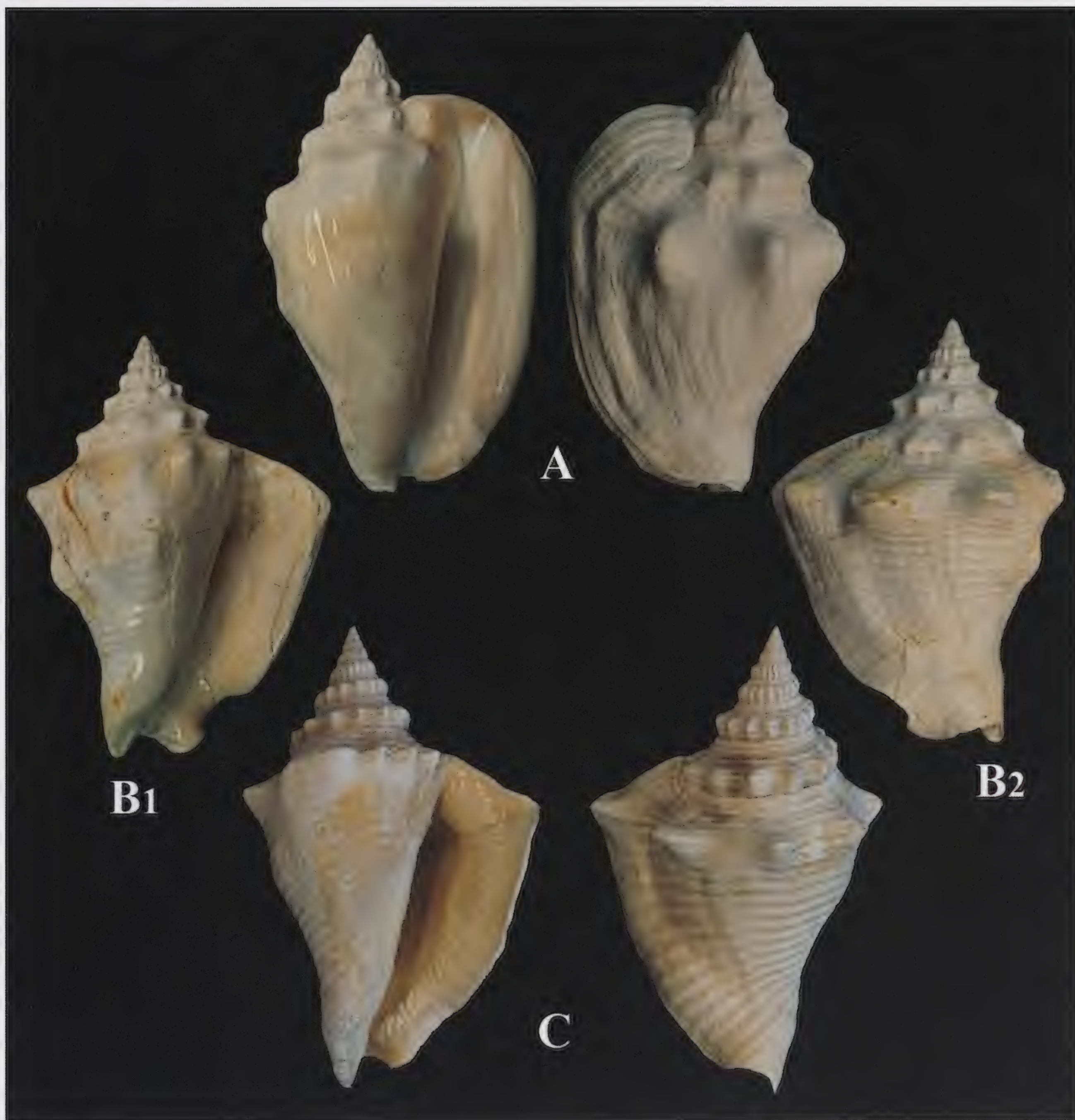
**Figure 4.** Extant members of *Persististrombus*, *Thetystrombus* and *Strombus*: **A** = *Persististrombus granulatus* (Swainson, 1821) – Manabi, Equador, 72 mm (collection Stephen Maxwell); **B** = *Thetystrombus latus* (Gmelin, 1791) – St Vincente Channel, Cape Verde Islands, 98 mm (collection Trevor and Marguerite Young); **C** = *Strombus alatus* Gmelin, 1791 – Marco Island, Florida, 84 mm (collection Stephen Maxwell); **D** = *Strombus gracilior* Sowerby, 1825 – Mexico, 71 mm (collection Stephen Maxwell); **E** = *Strombus pugilis* Linné, 1758 – Aruba, Dutch Antilles, 90 mm (collection Trevor and Marguerite Young); **F** = *Strombus worki* Petuch, 1983 – Brazil, 83 mm (collection Stephen Maxwell). Images not to scale.





**Figure 5.** Extant members of *Aliger*, *Lobatus*, *Macrostrombus* and *Titanostrombus*: **A** = *Aliger gallus* (Linné, 1758) – Porto Segura, Brazil 90 mm (collection Stephen Maxwell); **B** = *Aliger gigas* (Linné, 1758) – Dominican Republic, 306 mm (collection Jeroen Braakman); **C** = *Lobatus peruvianus* (Swainson, 1823) – Islas Cocinas, Mexico, 93 mm (collection Stephen Maxwell); **D** = *Lobatus raninus* (Gmelin, 1791) – Honduras, 51 mm (collection Stephen Maxwell); **E** = *Macrostrombus costatus* (Gmelin, 1791) – Bahamas, 110 mm (collection Stephen Maxwell); **F** = *Titanostrombus galeus* (Swainson, 1823) – West Panama 198 mm (collection Jeroen Braakman); **G** = *Titanostrombus goliath* (Schröter, 1805) – Ceará, Brazil, 316 mm (collection Jeroen Braakman). Images not to scale.





**Figure 6.** Fossil *Edpetuchistrombus* and *Antestrombus* species. **A** = *Edpetuchistrombus aldrichi* (Dall 1890) – Ten Mile Creek, Florida, 53 mm (Aart Dekkers Collection no. STR9470); **B** = *Antestrombus chipolanus* (Dall 1890) – Ten Mile Creek, Florida, 62 mm (Aart Dekkers Collection no. STR9469); **C** = *Antestrombus mardiaee* (Petuch 2004) – Ten Mile Creek, Florida, 42 mm (Aart Dekkers Collection no. STR9468). Images not to scale.



**An Examination of the Relationships Between Extant *Dolomena* Wenz, 1940, *Doxander* Wenz, 1940, *Mirabilistrombus* Kronenberg, 1998, *Neodilatilabrum* Dekkers, 2008 and *Labiostrombus* Oostingh, 1925 (Stromboidea: Neostromboidae: Strombidae)**

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**ABSTRACT** This paper presents an examination of the relationships between *Dolomena*, *Doxander*, *Mirabilistrombus*, *Neodilatilabrum* and *Labiostrombus* using character state analysis and maximum parsimony. Hypothesized relationships are presented through the introduction of definitions that bridge the understanding of the evolutionary relationships with the applied nomenclature. Dolomenini is introduced to incorporate two new subtribes: Dolomenina which combines parts of *Dolomena* ex Abbott (1960) and *Labiostrombus*; and Doxanderina, which encloses *Doxander* and *Neodilatilabrum*. Based on the generated phylogeny, *Amabiliplicatus*, *Pacificus* and *Dominus* are introduced, while *Ministrombus* is validated as monophyletic. The clustering of *Neodilatilabrum* and *Doxander* within Doxanderina, and the nesting of *Labiostrombus* within the Dolomenini are major revisions to Stromboid systematics.

**KEY WORDS** Character State, Gastropoda, Mollusca, Doxanderina, Dolomenini PhyloCode

## INTRODUCTION

The process of ordering nature is one of continual revision and change, especially when a great many new taxa are circumscribed within a small complex of organisms, or groups have been subjected to taxonomic inflation. Many of the discrete complexes that Abbott (1960) recognised 60 years ago within Strombidae Rafinesque, 1815 have been inflated, and now stand alone as independent genera. Notwithstanding the elevation of these subgenera, the relationship between these taxonomic entities has yet to be tested. Recent revisions that have targeted stromboids have mainly focused on the circumscription of new taxa (Man in't Veld and Visser 1993; Willan 2000; Visser & Man in't Veld 2005; Liverani

2013; Thach 2016), or the revaluation of existing genera (Bandel 2007; Dekkers 2008, 2010). Yet fundamentally, there have been few attempts at determining the phylogenetic relationships between these stromboid taxa. Where resolution has been attempted, there has been no attempt to impart the cladistic findings to the practical way nature is perceived, that is in the nomenclature (Latiolais *et al.* 2006).

*Dolomena* Wenz, 1940, *Doxander* Wenz, 1940 and *Labiostrombus* Oostingh, 1925 were once considered subgenera of *Strombus* Rafinesque, 1815, but have now all been elevated to genera. The elevation of these taxa, and the circumscription of new genera such as *Margistrombus* Bandel, 2007 (= *Neodilatilabrum* Dekkers, 2008), rather than as



subgenera within *Dolomena*, has resulted on the loss of the overarching relational meaning. Meaning that was once contained in the nomenclature and evidenced as a consequence of rank or subordinate taxa relationships before the age of taxonomic inflation of the subordinate ranks, particularly well-illustrated in the shift of subgenera to genera in Strombidae.

*Dolomena* are all medium-sized, distributed throughout the Indo-Pacific, and with their maximum diversity centred in the coral triangle. While these groups have also undergone a continual process of accretion into the genus *Dolomena* due to new circumscriptions of taxa, there has been no attempt at deciphering the relationships between taxa apart from the gross morphological similarity used only in the context of discriminating taxa (Man in't Veld and Visser 1993; Willan 2000; Visser & Man in't Veld 2005; Liverani 2013; Thach 2016). The presently assigned taxa to *Dolomena* still largely follow the historical arrangements outlined in Abbott (1960), although some species were later assigned to new genera such as *Neodilatilabrum* recognizing some of the natural divisions of Abbott (1960). Abbott (1960) arranged these taxa in a logical order based on similarity in shell characters: *Strombus plicatus* (Röding, 1798) complex (extant species pp. 89 – 92; extinct species p. 92- 93); *Strombus dilatatus* Swainson, 1821 complex (extant species pp. 93-94; extinct species pp. 95); *Strombus labiosus* Wood, 1828 complex (extant species 95-97; extinct species p. 97); *Strombus marginatus* Linnaeus, 1758 complex (extant species pp. 97-102; extinct species pp. 102 – 103); and the *Strombus variabilis* Swainson, 1820 grouping which includes *Strombus minimus* Linnaeus, 1771 (extant species 103-106; extinct species: none). However, Abbott (1960) presents no clear methodological approach to understanding the relationships

between the taxa he linked together, nor presented any justification other than similarity in form for his species justification. This led to a gross over simplification of the diversity presented before him (Maxwell *et al.* 2019a, b). Therefore, we aimed to bring a higher level of resolution of the genera and their relationships within the Strombidae using phylogenetic relationships to demonstrate that nomenclature can reflect the current evolutionary understanding within that complex rather than the simple aggregation of taxa based on uncritical analysis of form alone.

## ABBREVIATIONS

SMC – Stephen Maxwell Collection, Cairns, Queensland, Australia.

AMD – Aart Marius Dekkers Collection, Purmerend, the Netherlands.

## METHODS

The target taxa of this study were the members of the *Dolomena* Wenz, 1940 ex Abbott (1960) complex and the newly circumscribed taxa ascribed to that genera and its modern derivatives. *Laevistrombus* Abbott, 1960 (*Laevistrombus vanikorensis* (Quoy & Gaimard, 1834)), *Mirabilistrombus* Kronenberg, 1998 (*Mirabilistrombus listeri* (Gray, 1852)), *Doxander* (*Doxander vittatus* (Linnaeus, 1758)) and the monotypic *Labiostrombus* (*Labiostrombus epidromis* (Linnaeus, 1758)) were selected as outgroups based on the DNA sequence based phylogeny contained in Latiolais *et al.* (2006), these also share a general structural form and spatiotemporal similarity and were included to test their relationship with the focus genera, *Dolomena* (Abbott 1960; Kronenberg 1998; Maxwell *et al.* 2019a, b).

All species attributed to *Dolomena* Wenz, 1940 ex Abbott (1960) and its subsequent taxonomic



derivatives were considered, the types for the outgroups were examined, and twenty-three characteristics were coded based on this examination (Table 1). We focus on three regions of the shell for character coding. The first region included the aperture and columella, which fall into three subcategories (see Table 1) namely: the outer lip including the labellum and shape of the stromboidal lobe (Characteristics 1-4, and 12; Figure 1); the shape of the columella (Characteristics 5-7; Figure 1); and the shape of the posterior sinus (Characteristics 8-11; Figure 1). The second region dealt with the shape of the ventral body whorl (Characteristics 13-17; Figure 1). The third set of characters was drawn from the dorsal body whorl (Characteristics 18-21; Figure 1) and the dorsal spire (Characteristics 22-23; Figure 1). We used MEGA X (Kumar *et al.* 2018) to analyse morphological characters inferring the maximum parsimony phylogeny using a Max-mini branch and bound method. The generation of the phylogeny occurred in two phases. The first, at the rank of genera using the type species. When the outgroups *Doxander* Wenz, 1940 and *Labiostrombus* Oostingh, 1925 were found to be nested within the *Dolomenini tribus nov.*, all species contained within those nested taxa were included in the second round of analysis. This process avoided the algorithm inferring homologies at the rank of genera leading to distortion in the internal resolution of the phylogeny. The stability of all trees generated was undertaken using 500 bootstrap replications. Synapomorphies were then examined in terms of the fossil record and the phylogeny generated. We then demarcated relationships based on the phylogeny and defined them under the guidelines of the PhyloCode (2014). Where identified clades from the character analysis reflected the historical generic affiliation, the existing taxonomy was retained. Material examined to determine character sets were incorporated within the assigned taxa lists.

## SYSTEMATICS

*Dolomenini tribus nov.* was found to contain two distinct subclades (Figure 2A): the first, *Doxanderina subtribus nov.* contained monophyletic *Doxander* and *Neodilatilabrum* Figure 2B; and the second *Dolomenini tribus nov.*, contained monophyletic *Dolomena*, *Labiostrombus*, *Amabiliplicatus gen. nov.*, *Pacificus gen. nov.* and *Dominus gen. nov.* and *Ministrombus* (Figure 2C). The clustering of *Neodilatilabrum* and *Doxander* within *Doxanderina subtribus nov.*, and the nesting of *Labiostrombus* within the *Dolomenini tribus nov.* are major revisions in Stromboid systematics.

Phylum	Mollusca Linnaeus, 1758
Superorder	Caenogastropoda Cox 1960
Order	Sorbeoconcha Ponder & Lindberg, 1987
Superfamily	Stromboidea Rafinesque, 1815
Epifamily	Neostromboidae Maxwell, Dekkers, Rymer & Congdon, 2019
Family	Strombidae Rafinesque, 1815

### *Dolomenini tribus nov.*

**Type Genus.** *Dolomena* Wenz, 1940, p. 945.

**Definition.** The clade has the characteristics outlined in the diagnosis, and contains *Dolomena* Wenz, 1940, *Doxander* Wenz, 1940, *Labiostrombus* Oostingh, 1925 and *Neodilatilabrum* Dekkers, 2008 and taxa more closely related to them than to other members of Strombidae Rafinesque, 1815.

**Diagnosis.** Early to mid-teleoconch with even axial ornamentation. Outer lip without ornamentation, anterior canal short, shoulder of body whorls with knobs that may be greatly reduced.

**Etymology.** Based on the genus group name *Dolomena* Wenz, 1940.



***Doxanderina subtribus nov.***

(Figure 3)

**Type Genus.** *Doxander* Wenz, 1940, p. 945.**Definition.** The clade has the characteristics outlined in the diagnosis, and contains *Doxander* and taxa more closely related to it than members of the Dolomenina new subtribe.**Diagnosis.** The aperture of the shell is uniformly lirate. There is no marginal fold present on the edge of the outer lip. The outer lip lacks sharpness. The body of the shell is rounded, with a convex flange that may be stepped. There is no flange fold. The spire is sculptured with uniform axial ribs. The columella is straight and mostly smooth. The posterior sinus has uneven sides with the outer side being sharp-edged.**Etymology.** The name is based on the genus group name *Doxander* Wenz, 1940.***Doxander* Wenz, 1940**

(Figures 3A-E)

**Type Species.** *Strombus vittatus* Linnaeus, 1758, p. 545, no. 439 (Wenz, 1940, p. 945).**Definition.** The clade has the characteristics outlined in the diagnosis, and contains all recent members of the *Doxanderina subtribus nov.* not included within *Neodilatilabrum* Dekkers, 2008.**Original Description.** "Gehäuse groß bis sehr groß, schlank, spindelförmig; Gewinde hoch; Umgänge gewölbt, mit schmalem, glattem Streifen unter der Naht und axialen Rippen; Endwindung fast glatt oder mit mehr oder weniger deutlichen axialen Rippen, auf der unteren Hälfte mit Spiralrillen" (Wenz 1940, p. 945). [Translation: Shell large to very large, slender, spindle-shaped; high spire; whorls rounded, with small spiral lines under the suture and axial ribs; body whorl almost smooth or with distinct axial ribs on the lower half with spiral grooves].**Diagnosis.** Shells with a high spire. The body whorl is smooth or with strong axial folds or spiral lines. The dorsum is often with a central knob on the shoulder. The subsutural cord is well defined. The inside labrum has weak or stronger lirae. Stromboidal notch moderately well formed. The flange is stepped.**Synonymy.** Not *Doxander* Iredale (1931, p. 212): the changing of the ICZN (1985; 1999 Article 13.1) made the name unavailable as Iredale (1931) gave only a name without description. Thus, the name remained a *nomen nudum* until redescribed by Wenz (1940).**Assigned Taxa:***Strombus (Doxander) vittatus apicatus* Man in 't Veld and Visser, 1993, p. 19, pl. 2, figs. 1-6 [= *Strombus (Doxander) vittatus vittatus* form *australis* Schröter, 1805 ex Abbott (1960, p. 113)]. Type Locality: Brunei, Borneo, Kuala Belait (Man in 't Veld and Visser 1993) (Figure 3A). Material examined. THAILAND - Trawled Gulf of Thailand (SMC x 6), Bun Hua Him, Gulf of Thailand (AMD x 1), off Phuket Island (AMD x 1); VIETNAM - off Nha Trang (AMD x 1; SMC x 3).*Strombus campbelli* "Gray" Griffith and Pidgeon, 1834, p. 600, pl. 25, fig. 6 [= *Strombus (Doxander) vittatus campbelli* Griffith and Pidgeon, 1834 ex Abbott (1960, p. 113, pl. 17, fig. 18)]. Type Locality: Bowen, Queensland (Abbott 1960) (Figure 3B). Material examined: AUSTRALIA - Yirrkala, Gove, Northern Territory (SMC x 1), Amity Point, Stradbroke Island, Queensland (SMC x 2), Bountiful Island, Gulf of Carpentaria, Queensland (SMC x 1), Alexandra Reef, Queensland (SMC x 1), Cape York Peninsula, Queensland (SMC x 2), Dalrymple Point, Bowen, Queensland (SMC x 1), Dingo Beach, Queensland (AMD x 5; SMC x 91), Fraser Island, Queensland (SMC x 6), Gloucester Passage, Queensland (AMD x 2; SMC x 5),



Horseshoe Bay, Magnetic Island, Queensland (SMC x 3), King Reef, Queensland (SMC x 3), Kurrimine Beach, Queensland (AMD x 1; SMC x 6), Pallaranda, Queensland (SMC x 1), Pancake Creek, Queensland (SMC x 1), S.E. Mooloolaba, Queensland (SMC x 1), Saunders Beach, Queensland (SMC x 9), Shellbourne Bay, Queensland (SMC x 1), Shelly Beach, Townsville, Queensland (SMC x 14), Shoal Point, Mackay, Queensland (AMD x 2; SMC x 2), Thursday Islands, Torres Straits, Queensland (SMC x 1), Trawled off Townsville, Queensland (SMC x 19), Wonga Beach, Queensland (SMC x 2), Cape Kerau Dren, Western Australia (SMC x 1), Dampier Archipelago, Western Australia (AMD x 1), Jarman Island, Wickham, Western Australia (SMC x 3), Port Headland, Western Australia (AMD x 3; SMC x 2), Reginald Bay, Western Australia (SMC x 1), Rowley Shoals, Western Australia (SMC x 1), Shark Bay, Western Australia (AMD x 1; SMC x 2), Town Beach, Broome, Western Australia (SMC x 6).

*Strombus (Doxander) vittatus entropi* Man in't Veld and Visser, 1993, p. 26, pl. 2, figs. 7–12 [= *Strombus (Doxander) vittatus vittatus* Linnaeus, 1758 fide Abbott (1960, p. 111, pl. 17, fig. 14)]. Type Locality: Cañacao Bay, Sangley Point, Manila Bay, Luzon Island (after the holotype locality- Man in't Veld and Visser 1993). Material examined: MALAYSIA - Kudat, Sabah (AMD x 1); PHILIPPINES - Aliguat Island (SMC x 1), Bohol (AMD x 2), Matuban Island (AMD x 1), Masbate (AMD x 2), Calituban Island (SMC x 4), Davao (SMC x 21).

*Strombus japonicus* Reeve 1851, pl. 17 [= *Strombus (Doxander) vittatus japonicus* Reeve, 1851 fide Abbott (1960, p. 113, pl. 17, fig. 18)]. Type Locality: Nagasaki, Japan (Abbott 1960) (Figure 3D). Material

examined: JAPAN - Chiba (SMC x 1), Mikawa Archi prefecture (AMD x 1), Kii Straits (AMD x 3), Tosa Bay (AMD x 3).

*Strombus vittatus* Linnaeus, 1758, p. 545, no. 439 [= *Strombus (Doxander) vittatus vittatus* Linnaeus, 1758 ex Abbott (1960, p. 111)]. Type Locality: Ambon, Indonesia (Abbott 1960) (Figure 3E). Material examined: AUSTRALIA - Bountiful Island, Gulf of Carpentaria, Queensland (SMC x 2), Buchans Beach, Queensland (SMC x 1), Cape York Peninsula, Queensland (SMC x 1), Cook Reef, Torres Straits, Queensland (SMC x 1), Dingo Beach, Queensland (SMC x 19), Four Mile Beach, Port Douglas, Queensland (SMC x 2), Off Gladstone, Queensland (AMD x 3), Hinchinbrook Island, Queensland (AMD x 1), Keppel Bay, Queensland (SMC x 1), Kurrimine Beach, Queensland (SMC x 2), Moreton bay, Queensland (AMD x 1), Palm Island, Queensland (SMC x 1), Saunders Beach, Queensland (SMC x 2), Shelly Beach, Townsville, Queensland (SMC x 2), Shoal Point, Mackay, Queensland (SMC x 2), Stradbroke Island, Queensland (AMD x 1), Trawled off Townsville, Queensland (SMC x 3).

### ***Neodilatilabrum* Dekkers, 2008**

(Figures 3F-K)

**Type Species.** *Strombus marginatus* Linnaeus, 1758, p. 744, no. 431 (Dekkers, 2008).

**Definition:** The clade has the characteristics outlined in the diagnosis, and contains all recent members of the *Doxanderina nov. subtribus* not included within *Doxander* Wenz, 1940.

**Original Description.** “Shell small to medium sized, solid shells. Form of shell elongated. Spire medium to tall, body whorl not much decorated; the shoulder with a keel or evolved to a more round shoulder. Columella and aperture smooth, but inside of the not much



flaring lip decorated with little knobs. A stromboid notch is present” (Dekkers 2008, p. 58).

**Diagnosis.** Stromboidal notch sinuous. The flange is not stepped. Spire with distinct shoulder with knobs. Body whorl shiny and almost without any sculpture; expanded outer lip thickened at the inner edge and smooth. Aperture smooth within. Columellar smooth, with callous, well-marked. The anterior canal is short. The stromboid notch is moderately developed. The posterior canal is present.

**Synonymy.** *Margistrombus* Bandel, 2007, p. 153 is not accepted as valid under ICZN (1999) Article 13.1.1: “To be available, every new name published after 1930 must satisfy the provisions of Article 11 and must be accompanied by description or definition that states in words characters that are purported to differentiate the taxon”. However, Bandel (2007) described the selected type species. That is not fulfilling the strict requirements of Article 13 and therefore his proposed generic names are unavailable.

**Assigned taxa:**

*Strombus marginatus* Linnaeus, 1758, p. 744, no. 430 [= *Strombus (Dolomena) marginatus marginatus* Linnaeus, 1758 ex Abbott (1960, p. 98, pl. 18, figs. 6, 7)]. Type Locality: Sri Lanka (Abbott 1960) (Figure 3G). Material examined: INDIA - (SMC x 1), Cuddalore (AMD x 1), Deuipatnam (SMC x 1), Gulf of Bengal (AMD x 2), Kilakari (SMC x 1), Kilarkarai (SMC x 1), (AMD x 2), Kottai Pattanam (AMD x 8), Off Madras (AMD x 1; SMC x 1), Rameswarum (AMD x 1), Off Tondi (AMD x 1); SRI LANKA - Galle (AMD x 1), Trincomalee (AMD x 1; SMC x 2).

*Strombus robustus* Sowerby, 1875, p. 599, pl. 72, figs. 5, 5a. Type Locality: Hong Kong (Abbott, 1960) (Figure 3F). Synonym: *Margistrombus boucheti* Thach, 2016, pp. 39 – 40, fig. 2. Type Locality: Nha Trang

area, Khan Hoa Province, Vietnam (Thach 2016) (Figure 3F). Material examined: JAPAN - Bay of Tanabe (AMD x 1); SINGAPORE - Changi Coast Road (AMD x 1).

*Strombus septimus* Duclos, 1844, p. 7, pl. 13, figs. 9, 10 [= *Strombus (Dolomena) marginatus septimus* Duclos, 1844 ex Abbott (1960, p. 101, pl. 18, figs. 10, 11)]. Type Locality: Lusong, Luzon Island, Philippines (Abbott 1960) (Figure 3I). Material examined: MICRONESIA - Anguar, Palau (AMD x 1); PAPUA NEW GUINEA - (SMC x 3), Rabaul (AMD x 1); PHILIPPINES - Balicasag Island (SMC x 1), Bohol (AMD x 3), Garidad, Panay (AMD x 1), Luxon Island (AMD x 1), Manila Bay (AMD x 1), Negros Islands (AMD x 6); SOLOMON ISLANDS - Marapa Island (AMD x 1), Marau Sound (AMD x 2), Guadalcanal (AMD x 1); TAIWAN - Off Anping (AMD x 1); VANUATU - Vanuatu (AMD x 1).

*Margistrombus simanoki* Liverani, 2013, p. 77, pl. 1, figs. 1, 2. Type Locality: Tapaktuan, Aceh Province, northern end of Sumatra Island, Indonesia (Liverani 2013) (Figure 3J). Material examined: The photos from original publication: none in collections.

*Strombus (Dolomena) marginatus sowerbyorum* Visser & Man in't Veld, 2005, p. 58, Pl. 1, figs. 3,4; pl. 2, fig. 2; pl. 3, figs. 3, 4. [= *Strombus (Dolomena) marginatus robustus* Sowerby, 1874 (sic = 1875) ex Abbott (1960, p. 100, pl. 18, figs. 13, 14)]. Type Locality: Borneo, Brunei, Kuala Belait. ex coll. J.N.J. Post (Visser & Man in't Veld, 2005) (Figure 3H). Material examined: INDONESIA - (SMC x 1); TAIWAN: (SMC x 1); THAILAND - East Coast (SMC x 2); PHILIPPINES - Cebu Island (SMC x 1), Corregidor Island (SMC x 1); JAPAN – Kominato Chib (SMC x 4), Okinawa (SMC



x 4); VIETNAM - An Dang Beach (AMD x 2), Mui Ne (AMD x 1).

*Strombus succinctus* Linnaeus, 1767, p. 1212, no. 509 [= *Strombus* (*Dolomena*) *marginatus succinctus* Linnaeus, 1767 ex Abbott (1960, p. 99, pl. 18, figs. 13, 14)]. Type Locality: Madras, India (Abbott 1960) (Figure 3J). Material examined: INDIA - (AMD x 1), Cuddalore (AMD x 1), Kottai Pattinam (AMD x 5), Madras (AMD x 13; SMC x 5), Tuticorin (AMD x 2); SRI LANKA - Galle (AMD x 1), Lavinia (AMD x 1).

### ***Dolomenina subtribus nov.***

(Figure 4)

**Type Genus.** *Dolomena* Wenz, 1940, p. 945.

**Definition:** The clade has the characteristics outlined in the diagnosis, and contains *Dolomena* Wenz, 1940, and all taxa more closely related to it than members of *Doxander* Wenz, 1940, and *Neodilatilabrum* Dekkers, 2008.

**Diagnosis.** Shell with uniform spiral sculpture of fine axial ribs. The flange is convex, and a flange fold runs from the posterior end of the labrum to the anterior end, mostly following the outline of the outer edge of the labrum, and only becoming obsolete at both ends.

**Etymology.** Based on the genus group name *Dolomena* Wenz, 1940.

### ***Dolomena* Wenz, 1940**

(Figures 4A-C)

**Type Species.** *Strombus pulchellus* Reeve, 1851, fig. 52.

**Definition.** This clade has the characteristics outlined in the diagnosis, and contains *Strombus pulchellus* Reeve, 1851, and all taxa more closely related to it than the defining members of any other clade within *Dolomenina subtribus nov.*

**Original Description.** "Gehäuse mittelgroß, breiter; Außenrand der Mündung besonders oben mehr ausgebreitet; Endwindung mit einer weiteren, tieferstehenden Reihe kleiner Höcker" (Wenz 1940, p. 945) [Translation: Shells of medium size, broader; outer lip especially broader at the posterior end; body whorl with a second lower row of small knobs].

**Diagnosis.** Shells from 2 cm to 6 cm. Spire with distinct shoulder and with knobs mostly axially aligned. Body whorl with small knobs dorsally and spiral ribbing that can become obsolete. A hardly noticeable second row of very small knobs is present at the mid-whorl, where the outline of the shell has a nick. Expanded outer lip broader at the posterior end and flattened toward the rim. Aperture lirate within, stained with brown colour entering the aperture. Columellar callous present but small on the ventral side, marked, with lirae at the upper half, which are white or brown coloured. A brown background colour is often found deeper within the aperture. Lower half of the columella smooth and with thickened callous. Anterior canal short but always longer than the anterior part of the outer lip. Deeply incised stromboid notch.

**Synonymy.** *Dolomena* Wenz, 1940, p. 945 [Not *Dolomena* Iredale (1931, p. 212): the changing rules of the ICZN (1999) made the name unavailable as Iredale (1931) gave only a name without description. Thus, the name remained a *nomen nudum* until the first description was provided by Wenz (1940)].

### **Assigned Taxa:**

*Strombus columba* Lamarck, 1822, p. 208 [= *Strombus* (*Dolomena*) *plicatus* subspecies *columba* Lamarck, 1822 ex Abbott (1960, p. 90, pl. 18, figs. 1, 2)]. Type locality: Zanzibar (Abbott 1960) (Figure 4A). Material examined: MOZAMBIQUE - Nacala Bay (AMD x 5; SMC x 1); SEYCHELLES - Mahe (AMD x 1), Off



Victoria, Mahe (AMD x 2); TANZANIA - (AMD x 1); Nungi, Zanzibar (AMD x 1).

*Strombus (Labiostrombus) hickeyi* Willan, 2000, p. 20, pl.1, figs. 1, 2. Type locality: Bowen, Queensland (Willan 2000) (Figure 4B). Material examined: AUSTRALIA - Bowen Sand Flats, Queensland (SMC x 1), Dingo Beach, Queensland (AMD x 4; SMC x 9), Green Island, Queensland (SMC x 1), Palm Island, Queensland (AMD x 1; SMC x 2), Shellbourne Bay, Queensland (SMC x 1).

*Strombus pulchellus* Reeve, 1851, fig. 52 [= *Strombus (Dolomena) plicatus* subspecies *pulchellus* Reeve, 1851 ex Abbott (1960, p. 92, pl. 63, fig. 2)]. Type Locality: Philippines (Abbott 1960) (Figure 4C). Material examined: AUSTRALIA - Dingo Beach, Queensland (SMC x 1), East of Noosa, Queensland (SMC x 2), Dampier, Western Australia (SMC x 1); CHINA - South of Palau Subi Besar (AMD x 2); INDIA - Off Chennai (AMD x 2), Off Ervadi SE Coast (AMD x 1), Tuticorin (AMD x 2); INDONESIA - Wasir Island (SMC x 1); NEW CALEDONIA - Gue Reef (AMD x 10); PAPUA NEW GUINEA - Rabaul (AMD x 2; SMC x 1), Samuray (AMD x 1); PHILIPPINES - Aliquay (AMD x 5), Balicasag Island (AMD x 2), Balut Island (AMD x 1), Birat and Kanipaan, Samal (AMD x 2), Bogo (SMC x 1), Bohol (AMD x 2), Calituban Island (AMD x 1), Cardidad, Panay (AMD x 1), Cebu Island (AMD x 1; SMC x 1), Davau Island (SMC x 1), Mactan (AMD x 1), Olango (AMD x 6), Palawan (AMD x 1), Samar (AMD x 1), Santa Rosa Island, Cebu (AMD x 1), Tinina Balut Island (SMC x 1); MALAYSIA - Kudat, Sabah (AMD x 1); MICRONESIA - Orote Point, Guam (AMD x 2); SOLOMON ISLANDS - Bonegi (SMC x 1), Honiara (SMC x 1), Kakabona, Guadalcanal (SMC x 1), Makina Passage (AMD x 2), Marau

Sound (AMD x 16); THAILAND - Port Dickson (AMD x 1).

### ***Labiostrombus* Oostingh, 1925** (Figure 4D)

**Type Species.** *Strombus epidromis* Linnaeus, 1758, p. 745, no. 436.

**Definition.** The characteristics outlined in the diagnosis, and contains *Strombus epidromis* Linnaeus, 1758, and all taxa more closely related to it than the defining members of any other clade within Dolomenina new sub tribe.

Original Description: "Genus XIII Gallinula § 164 Gallinis incubantibus adsimilamus Volutas gibbas acute muronatas; labia expanso instar alae; in acumen terminatas" (Klein 1753, p. 56). [Translation: as like a brooding chicken (sic) not unlike *Voluta gibbas* with a distinct point; flange expanded and wing like; terminating in a sharp point]. Oostingh (1925, p. 58) defined *Strombus (Labiostrombus)* as the replacement name for *Gallinula* "Kl" Mörch, 1852, p. 61 and gave attribution to "(Klein) Herrmannsen, 1847, H. & A. Adams, 1854" [non Brisson, 1760 - Aves].

**Diagnosis.** Shell with smooth aperture and columella. The outer lip has a marginal fold and is uniformly calloused towards the edge. The columella is straight. The dorsum has low small knobs or ribs. Spire uniformly sculptured with axial ribs.

**Synonymy.** *Gallinula* "Klein" Mörch 1852, p. 61.

### **Assigned Taxa:**

*Strombus epidromis* Linnaeus, 1758, p. 745, no. 436 [= *Strombus (Labiostrombus) epidromis* Linnaeus, 1758 ex Abbott (1960, p. 107, pl. 83, figs. 1, 2)]. Type Locality: Amboina, Indonesia (Abbott 1960) (Figure 4D). Material examined: AUSTRALIA - Trawled off Townsville, Queensland (SMC x 1), Broome, Western Australia (SMC x 1), Swains Reef (AMD x 1); INDONESIA -



Bengkulu, West Sumatra (AMD x 1), Pendangaran (AMD x 1); MALAYSIA - Sikuati, Sabah (AMD x 1); NEW CALEDONIA - Boats Pass (AMD x 2), Goeland Island (SMC x 1), Grande Goude (AMD x 1), Noumea (SMC x 1), Poum (AMD x 1), Thio (AMD x 6); CHINA - South China Sea (AMD x 1), THAILAND - Gulf of Thailand (SMC x 2); PAPUA NEW GUINEA - Kokopo (SMC x 2), Rabaul (AMD x 2), Tubesseria (AMD x 1); PHILIPPINES - Batayan Island (AMD x 1), Bohol (AMD x 2), Calituban Island (AMD x 1), Cebu (AMD x 1), Dumanhug (AMD x 2), Off Maya, Cebu (AMD x 1), Olango (AMD x 2), Placer, Masbate (AMD x 1), Siasi, Sulu Sea (AMD x 1); VANUATU - Vanuatu (AMD x 1).

### ***Ministrombus* Dekkers, 2010**

(Figures 4E-G)

**Type Species.** *Strombus minimus* Linnaeus, 1771, p. 549.

**Definition.** This clade has the characteristics outlined in the diagnosis, and contains *Strombus minimus* Linnaeus, 1771, and all taxa more closely related to it than the defining members of any other clade within *Supradolomina subtribus nov.*

**Original Description.** Shell “with pointed spire (40 degrees) with a median corner that bears nodes. The outer lip forms a lobe on a ridged end and is attached to the suture or above the body whorl. A thickened callus ridge of inner lip continuous to the posterior canal. The siphonal canal is wide and upturned. Shell size ranges from 20-65 mm” (Dekkers 2010, p. 9).

**Diagnosis.** The spire has a distinct shoulder with knobs. The body whorl is shiny and almost without any sculpture. The expanded outer lip is thickened at the inner edge and is shiny and smooth. The aperture is smooth within. The columellar is smooth, with a well-defined

callous. The anterior canal is short. The stromboid notch is medium deep. The posterior canal is present.

**Synonymy.** *Ministrombus* Bandel, 2007, p. 154, is not accepted as valid under ICZN (1999) Article 13.1 [see *Margistrombus* Bandel, 2007 above].

### **Assigned Taxa:**

*Strombus athenius* Duclos, 1844, p. 7, pl. 11, fig. 2 [= *Strombus (Dolomena) variabilis athenius* Duclos, 1844 ex Abbott (1960, p. 104, pl. 79, figs. 3, 4)]. Type Locality: Biak Island, Dutch New Guinea (= Indonesia, Abbott 1960) (Figure 5E). Material examined: AUSTRALIA - Green Island, Queensland (SMC x 1); PAPUA NEW GUINEA - New Britain (SMC x 2), Milne Bay (SMC x 4); NEW CALEDONIA - (SMC x 2), Arama (SMC x 1), Plage de Baffade (SMC x 3).

*Strombus minimus* Linnaeus, 1771, p. 549 [= *Strombus (Dolomena) minimus* Linnaeus, 1771 ex Abbott (1960, p. 105, pl. 18, figs. 2, 5)]. Type Locality: Cebu City, Philippines (Abbott 1960) (Figure 5F). Material examined: AUSTRALIA - James' Point, WA (AMD x 1); INDONESIA - Waiara, Flores (AMD x 4); NEW CALEDONIA - Beleps Islands (AMD x 1); NEW HEBRIDES - Vila (AMD x 3); PAPUA NEW GUINEA - Kokopo (SMC x 5), Port Moresby (SMC x 2); Rabaul (SMC x 5); PHILIPPINES - Bantagas (AMD x 1), Bohol (AMD x 1), Balabac Island (AMD x 1), Balicasag Island (SMC x 1), Batangas (AMD x 5), Bohol (AMD x 6), Palawan (AMD x 1), Punta Engano, Cebu (AMD x 1), Quezon (AMD x 1), Zamboanga (AMD x 1); SOLOMON ISLANDS - Ghizo Harbour (SMC x 1), Guadalcanal (AMD x 4; SMC x 1), Ngella Island (SMC x 2); VANUATU - (AMD x 4; SMC x 1).

*Strombus variabilis* Swainson, 1820, pl. 10 [= *Strombus (Dolomena) variabilis* subspecies



*variabilis* Swainson, 1820 ex Abbott (1960, p. 103, pl. 79, figs. 1, 2)]. Type Locality: Cebu, Philippines (Abbott 1960) (Figure 5G). Material examined: AUSTRALIA - Fairy Reef (AMD x 1), Swains Reef (AMD x 2); INDONESIA - Off Batu Belubang, NE Bangka Island (SMC x 1); JAPAN - East China Sea (AMD x 1); MALAYSIA - Guya Island, Sabah (AMD x 2), Kota Kinabalu, Borneo (AMD x 3), Kudat, Sabah (AMD x 1), Miri, Sarawak (AMD x 1); MARSHAL ISLANDS - Kwajalein (SMC x 6); PAPUA NEW GUINEA - Rabaul (AMD x 2); PHILIPPINES - Aliguay Island (SMC x 1), Balabac, Palawan (AMD x 2), Bohol (AMD x 1), Calituban Island (AMD x 1), Caubian Deep (AMD x 1), Cebu (AMD x 6), Dinagat Island, Surigao (SMC x 3), Don Island (SMC x 4), Maasin, Leyte (AMD x 1), Masbate (AMD x 6), Maya, Cebu (AMD x 2), Nocnocan Island (AMD x 1), Olango (AMD x 4), Pagbilao Bay (AMD x 4), Pandagang island (AMD x 1), Palawan (AMD x 2), Polilio Island (AMD x 4), Samar (AMD x 3), Sulu (AMD x 4), Talicud Island, Samal (AMD x 1); THAILAND - Bangirak (AMD x 1), Koh Mak (AMD x 7), Off Phuket (AMD x 2); TAIWAN - (AMD x 2); TONGA - Vavua Islands (AMD x 1).

***Amabiliplicatus* gen. nov.**

(Figures 4H-J)

**Type Species.** *Lambis plicata* Röding, 1798, p. 65, no. 835.

**Definition.** This clade has the characteristics outlined in the diagnosis, and contains *Lambis plicata* Röding, 1798, and all taxa more closely related to it than the defining members of any other clade within *Dolomenina subtribus* nov.

**Diagnosis.** The spire rather high with shallow knobs and infrequent old varices. The body whorl is broad, with spiral ribbing that becomes coarser towards the anterior end, with small

knobs rounded or stretched axially on the rounded shoulder. The shell has a broadly expanded outer lip. The aperture is coarsely lirated within, white or stained with brown. The columellar callous is present but small. The columella is fully lirated, often brown coloured on the lirae. The anterior canal is very short but broad. Strombus notch broad but shallow.

**Etymology.** The name is a combination of the Latin words *amibilis* meaning “lovely” and *plicatus* meaning “plicate” for the axially stretched ribbing on the dorsum of species belonging to this genus.

**Assigned Taxa:**

*Lambis plicata* Röding, 1798, p. 65, no. 835 [= *Strombus (Dolomena) plicatus plicatus* (Röding, 1798) ex Abbott (1960, p. 89, pl. 18, fig. 12)]. Type locality: Red Sea (Abbott 1960) (Figure 4H). Material examined: EGYPT - Abu Mad (AMD x 2), Hurghada (AMD x 1), Marsa Sleemet (SMC x 2), Ras Zafarana (AMD x 1).

*Strombus sibbaldi* Sowerby, 1842, p. 28, pl. 6, figs. 10, 11 [= *Strombus (Dolomena) plicatus sibbaldi* Sowerby, 1842 ex Abbott (1960, p. 91, pl. 18, fig. 15, 16)]. Type locality: Ceylon (= Sri Lanka, Sowerby 1842) (Figure 4I). Material examined: INDIA - Off Madras (AMD x 1), Kollam, Kerala (AMD x 3; SMC x 2), Rameswaram (AMD x 1), South East Coast (AMD x 1; SMC x 1), West Coast (SMC x 1).

*Strombus yerburyi* Smith, 1891, p. 419, pl. 33, fig. 5 [= *Strombus (Dolomena) plicatus sibbaldi* Sowerby, 1842 ex Abbott (1960, p. 92)]. Type locality: Gulf of Aden, Arabian Sea (Smith 1891) (Figure 4J). Material examined: DJIBOUTI - (AMD x 1); SOMALIA - (SMC x 3), Off Cape Guardafui, Suqutra Island (AMD x 1), Ras Hafun (AMD x 1), South of Mogadishu (AMD x 1), North Coast (AMD x 1); YEMEN - Aden (AMD x 1).



***Dominus gen. nov.***

(Figures 5A-C)

**Type Species.** *Strombus labiosus* Wood, 1828, p. 54, pl. 4, fig. 3.

**Definition.** This clade has the characteristics outlined in the diagnosis, and contains *Dolomena wienekei* Wiersma & Monsecour, 2012, and all taxa more closely related to it than the defining members of any other clade within *Dolomenina subtribus nov.*

**Diagnosis.** The spire with a distinct shoulder and knobs mostly axially aligned. The body whorl has medium knobs dorsally on the shoulder, and weak spiral ribs. The expanded outer lip has a strongly thickened end. The posterior outer lip is horizontal or pointing slightly upwards to the posterior. The aperture is lirate within. The columellar callous is mostly smooth or weakly lirate. The anterior canal is rather short.

**Etymology.** The name is derived from the Latin *dominus*, meaning “lord”.

**Assigned taxa:**

*Dolomena abbotti* Dekkers & Liverani, 2011, p. 111, pl. 1, fig. 6 and pl. 2, figs. 10-12 [= *Strombus (Dolomena) labiosus* Wood, 1828 ex Abbott (1960, p. 95, pl. 18, figs. 17-19)]. Type Locality: Phuket, Andaman Sea (Dekkers and Liverani 2011) (Figure 5A). Material examined: THAILAND - Kantang (AMD x 1), Korbon Island (AMD x 1), Ranong (AMD x 1), Rawai, Phuket (AMD x 1); INDONESIA - Off Sarni, Irian Jaya (AMD x 1), Off Racha Island, Andaman Sea (SMC x 1); MALAYSIA - Kota Kinabalu, Borneo (AMD x 1), Sedili, Johor (AMD x 2); PHILIPPINES - Bohol Island (SMC x 1), Cebu Island (SMC x 1); SINGAPORE - (AMD x 3).

*Dolomena wienekei* Wiersma & Monsecour, 2012a, p. 37 [= *Strombus (Dolomena) labiosus* Wood, 1828 ex Abbott (1960, p. 95, pl. 69, figs. 1, 2)]. See Wiersma &

Monsecour (2012b) for an amended description. Type Locality: Northern Coast of New Britain, Kimbe Plantation, Papua New Guinea (Wiersma & Monsecour 2012a) (Figure 5B). Material examined: PAPUA NEW GUINEA - Off Goodenough Island (AMD x 3), Rabaul (SMC x 3).

*Strombus labiosus* Wood, 1828, p. 54, pl. 4, fig. 3 [= *Strombus (Dolomena) labiosus* Wood, 1828 ex Abbott (1960, p. 95)]. Type Locality: Tuléar, west Madagascar (Dekkers & Liverani 2011) (Figure 5C). Material examined: MADAGASCAR - Tulear (AMD x 9; SMC x 1); MOZAMBIQUE - Pamba Island (AMD x 3), Seven Tree Island (AMD x 1); SRI LANKA - (AMD x 1).

***Pacificus gen. nov.***

(Figures 5D-F)

**Type Specie.** *Strombus dilatatus* Swainson, 1821, pl. 71.

**Definition.** This clade has the characteristics outlined in the diagnosis, and contains *Strombus dilatatus* Swainson, 1821, and all taxa more closely related to it than the defining members of any other clade within *Dolomenina subtribus nov.*

**Diagnosis.** The spire has a distinct (angular) shoulder with knobs axially aligned and spiral ribbing, old varices present. The body whorl has small knobs dorsally and faint spiral ribbing. The outer lip is expanded and flattened towards the edge. The inner lip is calloused at the edge. The aperture is lirate within. The posterior canal is present and bends towards the spire. The columellar callous is well formed, and lirate posteriorly and never coloured. The anterior canal is rather short but broad. Stromboid notch is broad and shallow.

**Etymology.** The name is derived from the Latin word *pacificus* meaning “peaceful”.



**Assigned Taxa:**

*Strombus dilatatus* Swainson, 1821, pl. 71 [= *Strombus (Dolomena) dilatatus dilatatus* Swainson, 1821 ex Abbott (1960, p. 93, pl. 66, fig. 2)]. Type Locality: Upala Cay (= Upolo Cay), Queensland, Australia (Abbott 1960) (Figure 5D). Material examined: AUSTRALIA - Bowen, Queensland (SMC x 3), Cape Morten, Queensland (SMC x 6), Dingo Beach, Queensland (AMD x 5; SMC x 16), East of Noosa, Queensland (SMC x 55), Gould Reef, Queensland (SMC x 2), Green Island, Queensland (SMC x 1), Keppel Bay, Queensland (AMD x 2; SMC x 1), North West Is. Capricorn Group, Queensland (SMC x 1), Off Sandy Cape, Queensland (AMD x 1; SMC x 2), Palm Island, Queensland (SMC x 8), Swains Reefs, Queensland (AMD x 3; SMC x 1), Townsville, Queensland (AMD x 2; SMC x 6), Trunk Reef, Queensland (SMC x 4); NEW CALEDONIA - Armama (SMC x 1); SOLOMON ISLANDS - (SMC x 1).

*Strombus orosminus* Duclos, 1844, p. 6, pl. 10, figs. 10, 11 [= *Strombus (Dolomena) dilatatus dilatatus* form *orosminus* Swainson, 1821 ex Abbott (1960, p. 93, pl. 66, fig. 2)]. Type Locality: Duclos, 1844 gave no type locality, nor did Abbott (1960); we hereby designate Olango Island, Philippines (Figure 5E). Material examined: PHILIPPINES - Davau Island (SMC x 1), Olango (AMD x 2), Mactan (AMD x 2).

*Strombus swainsoni* Reeve, 1850, figs. 28a, [= *Strombus (Dolomena) dilatatus swainsoni* Reeve, 1850 ex Abbott (1960, p. 94, pl. 66, fig. 1)]. Type Locality: Reeve, 1850 gave no locality, nor did Abbott (1960); we hereby designate Nha Trang, Khánh Hòa Province, Vietnam (Figure 5F). Material examined: VIETNAM - Danang (SMC x 1), Off Nha Trang (AMD x 10; SMC x 2); CHINA - South China Sea (AMD x 7).

**DISCUSSION**

The clade *Dolomenini tribus nov.* divides into two, *Dolomenina subtribus nov.* and *Doxanderina subtribus nov.*, whose characteristics are well established in the Pliocene and perhaps late Miocene. *Neodilatilabrum rutteni* (Altena, 1942) from the Pliocene of Java and *Pacificus togopiensis* (Cox, 1948) from the Pliocene of Java, are early members of *Doxandrina subtribus nov.*, both having straight and smooth columellas, a stepped in-curved flange and interior lirations typical of that clade. *Neodilatilabrum rutteni* is a fossil species with a sharp outer lip, triangulate shoulder, interior liration, and even its sculpture is not dissimilar to members of *Neodilatilabrum*, but it lacks the curved flange of *Doxanderina subtribus nov.* The recognition of *Dolomenina subtribus nov.* reflects its long fossil record in the Indo-Pacific. *Dominus fennemai* (Martin, 1899) and *Dominus teschi* (Cox, 1948) from the Pliocene of Indonesia show the straight flange with a folded, sinuous columella, and cuneate dorsal body whorl.

The recently described *Doxander bruneiensis* (Harzhauser *et al.*, 2018; Late Miocene, Borneo) is reassigned from *Dolomena* based on the subsutural cord, the simple outer lip and the strong lirae inside the labrum that is a characteristic diagnostic of the genus *Doxander*. It is most likely an early representative of that genus with a more compact shell; a form that evolved into the extant species that have a more elongated spire, with the diagnostic characters remaining unchanged.

The fossil *Labiostrombus denti* Cox, 1948 (Pliocene, Java) indicates that *Labiostrombus* has a long fossil record at least from the Miocene to the present day. Willan (2000) synonymized *Dolomena* with *Labiostrombus* Oostingh, 1925, and this debatable taxonomic



arrangement was not followed by subsequent authors (Bandel 2007; Dekkers 2008; Liverani 2013). Notwithstanding, we found that *Labiostrombus* was not nested with the wider *Dolomena* complex.

## CONCLUSION

The beauty of phylogenetic nomenclature is that these definitions can be redefined as our understanding of the internal structure improves. Notwithstanding future shifts in thinking, this paper provides a starting point for cladistic revisions that has been lacking in strombiod systematics in terms of re-evaluating the evolutionary relationships within the Stromboidea.

With the circumscription of *Dolomenini tribus nov.*, *Dolomenina subtribus nov.* and *Doxanderina subtribus nov.*, this study brings greater resolution to the internal structure of the Strombidae. Furthermore, this study demonstrated that, while the work of Abbott (1960; Jung and Abbott 1967) coalesced much of the historical taxonomy of Strombidae, the systematics contained within that work has led to a manifest limitation on the genus and species richness, and in particular, not yet recognized genera were ‘lost’ through a process of over-aggregation of similar taxa (Maxwell *et al.* 2018; Maxwell *et al.* 2019a). This has been resolved with the introduction of *Amabiliplicatus gen. nov.*, *Pacificus gen. nov.* and *Dominus gen. nov.*

## ACKNOWLEDGEMENTS

Our warm thanks go out to Thierry Backeljau (Belgium, Royal Belgian Institute of Natural Sciences) for proofreading and the many suggestions for improvements of the paper. We value his efforts and advices improving the article. The advice to use DNA was however not our study.

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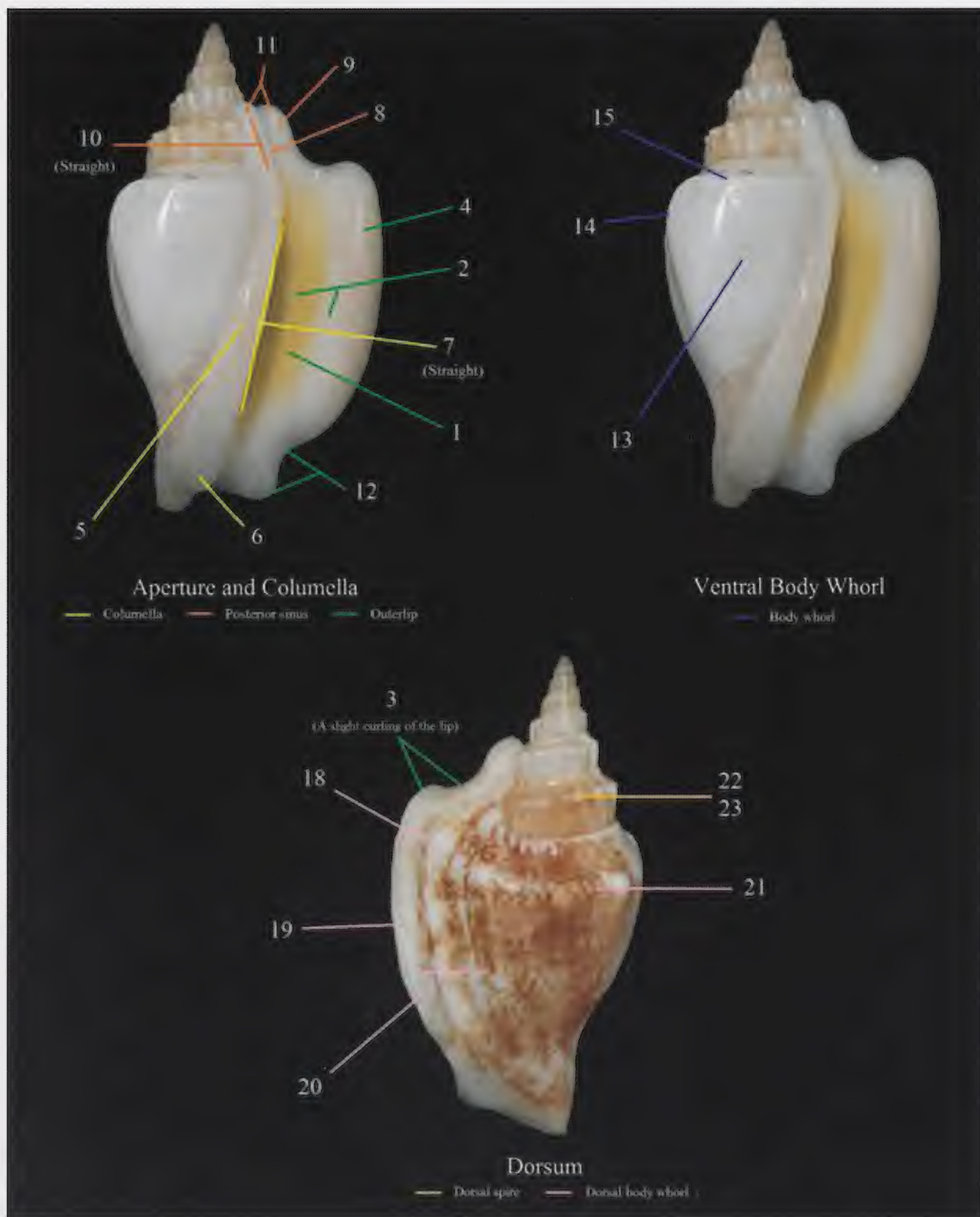
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<i>apicatus</i>	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	0	0	1	0	3	1	1
<i>athenius</i>	0	0	2	1	0	1	0	1	2	0	1	2	0	2	0	1	0	1	0	1	1	0	0
<i>campbelli</i>	1	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	0	1	0	1
<i>columba</i>	1	0	1	1	1	0	0	1	2	1	0	1	0	2	0	1	3	2	0	1	2	1	1
<i>dilatatus</i>	1	1	1	1	2	0	0	1	1	1	0	1	0	0	0	1	3	1	0	1	3	1	1
<i>entropi</i>	1	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	0	1	0	3	1	1
<i>epidromis</i>	0	0	2	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	2	0	1
<i>hickeyi</i>	1	1	1	1	2	0	0	1	2	1	0	1	0	2	0	1	3	2	0	1	2	0	1
<i>japonicus</i>	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	0	0	1	0	2	1	1
<i>kleckhamae</i>	1	1	1	1	2	0	0	1	1	0	1	2	0	0	1	0	0	0	1	0	2	1	1
<i>labiosus</i>	1	1	1	1	2	0	1	1	0	0	0	0	2	0	1	0	2	1	0	1	2	1	1
<i>listeri</i>	1	0	1	0	0	0	0	0	1	0	2	1	0	1	0	0	0	2	0	1	0	0	0
<i>marginatum</i>	1	1	0	0	0	0	0	0	1	0	0	0	3	1	1	0	1	0	0	0	4	1	0
<i>minimus</i>	1	0	2	1	2	1	0	0	2	0	1	2	0	2	0	0	3	2	0	1	2	0	1
<i>orosminus</i>	1	1	1	1	2	0	0	0	1	1	0	1	0	0	1	0	0	1	0	1	3	1	0
<i>plicatus</i>	1	0	1	1	1	0	0	1	0	0	0	2	1	0	0	2	3	1	1	1	3	0	1
<i>pulchella</i>	1	0	1	1	1	0	0	1	2	1	0	2	0	1	0	1	3	2	0	1	3	0	1
<i>robustum</i>	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	2	3	0	0	0	1	0	0
<i>septimum</i>	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0
<i>sibbaldi</i>	1	0	0	0	1	0	0	1	0	0	0	1	1	0	1	1	1	2	1	1	2	0	1
<i>simanoki</i>	1	0	0	0	0	1	0	1	1	1	0	0	1	0	0	1	3	0	0	0	1	1	1
<i>sowerbyorum</i>	1	1	0	0	0	0	0	0	1	1	0	0	1	2	0	0	0	0	0	0	1	1	0
<i>succinctum</i>	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0
<i>swainsoni</i>	1	1	1	1	2	0	0	0	1	1	0	1	0	0	1	0	0	2	0	1	3	1	0
<i>vanikoriensis</i>	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
<i>variabilis</i>	0	0	2	1	0	1	0	1	2	0	1	2	0	2	0	1	0	2	0	1	2	0	1
<i>vittatus</i>	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	0	2	0	0
<i>wienekei</i>	1	1	1	1	2	0	1	1	0	0	0	1	0	0	1	0	2	2	0	1	3	1	1
<i>yerburyi</i>	1	0	0	0	1	0	0	1	1	0	0	0	1	0	0	2	1	1	1	1	2	0	1
<sup>1</sup> Aperture – (1) The texture of aperture: 0 - smooth; 1 - lirate. (2) Uniformity sculptural form of inner labrum: 0 - no change in ornamentation; 1 - variable ornamentation. (3) Marginal fold: 0 - absent; 1 - indistinct; 2 - distinct. (4) Lip edge callous: 0 - no callosity; 1 - calloused. (5) Texture of the columella: 0 - smooth/indistinct; 1 - lirate; 2 - lirate posteriorly and/or anteriorly. (6) Columella callosity prior to the formation of the anterior canal: 0 - uniform callosity; 1 - thickened basally. (7) The form of the columella: 0 - straight; 1 - sinusoidal. (8) Posterior sinus: 0 - long; 1 - short. (9) Posterior sinus lobes: 0 - open canal; 1 - sharp outer lobe; 2 - calloused outer lobe. (10) Shape of posterior sinus: 0 - straight/ moderately straight; 1 - strongly recurved. (11) Both sides of sinus well developed; 0 - not even; 1 - even; 2 - not developed. (12) Stromboidal notch and lobe: 0 - sinuous; 1 - moderately well formed; 2 - well formed. <i>Ventral Body Whorl</i> - (13) Sculpture of the shield: 0 - smooth; 1 - with axial ribbing; 2 - with thick axial folds; 3 - fine uniform striations. (14) Acute ridge left side of shield: 0 - absent; 1 - indistinct; 2 - distinct. (15) Shape of shoulder: 0 - angulate; 1 - rounded. (16) Sculpture of the shoulder: 0 - smooth/one or two small nodules; 1 - sculptured; 2 - with uniform nodules. (17) Shape of body whorl: 0 - fusiform; 1 - biconically acute; 2 - anteriorly cuneate; 3 - Quatrately fusiform. <i>Dorsal body whorl</i> - (18) Flange fold: 0 - absent; 1 - indistinct; 2 - distinct. (19) Flange: 0 - not stepped; 1 - uniformly stepped. (20) Cross sectional shape of flange: 0 - convex; 1 - straight. (21) Shoulder sculpture: 0 - smooth; 1 - with one or two faint knobs; 2 - distinct knobs; 3 - ribs; 4 - keeled. <i>Dorsal Teleoconch</i> - (22) Penultimate whorl spiral sculpture: 0 - smooth/ indistinct; 1 - with fine striations. (23) Penultimate whorl axial sculpture: 0 - smooth; 1 - uniformly plicate.																							

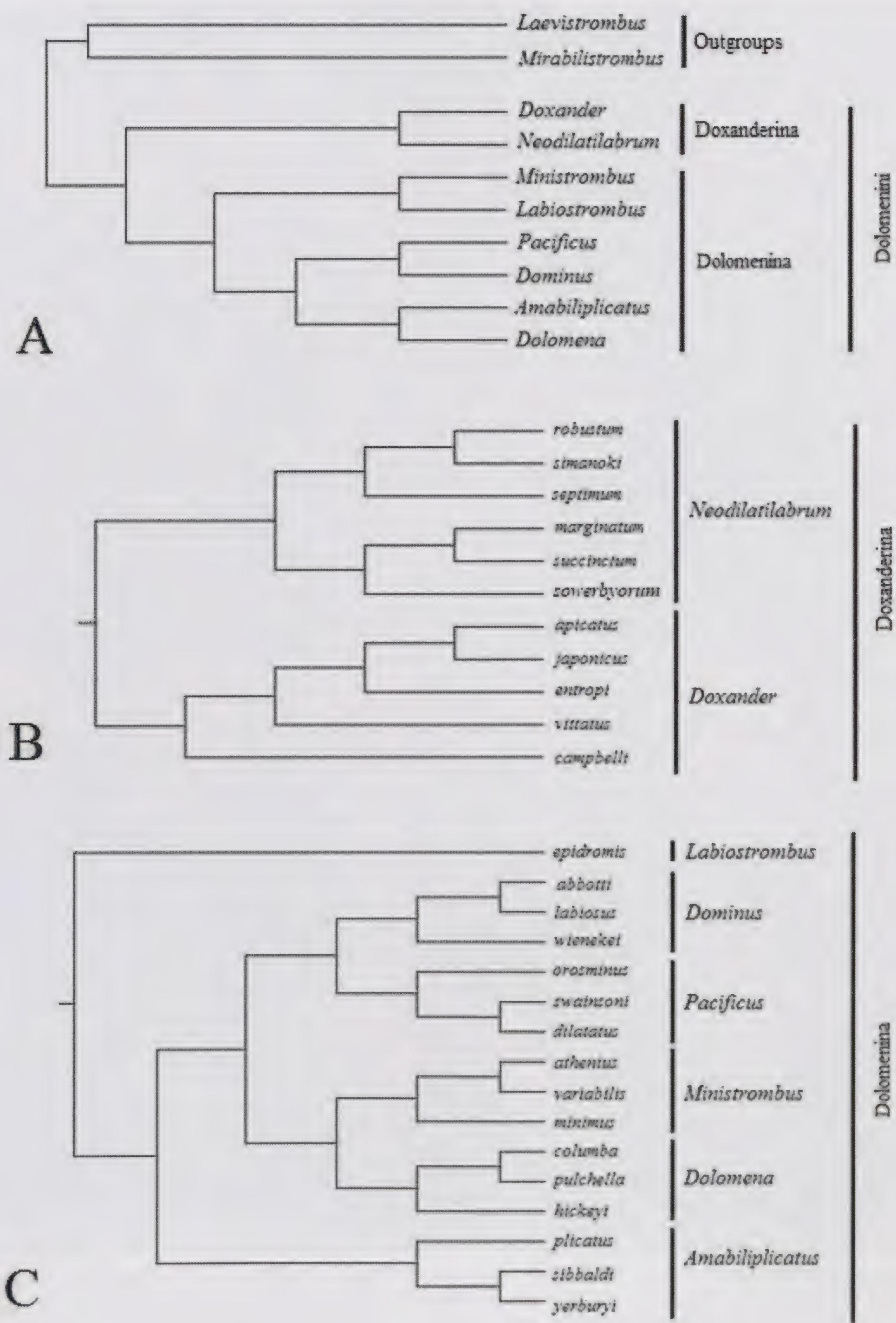
Table 1. Character states for typical representatives of each taxon.





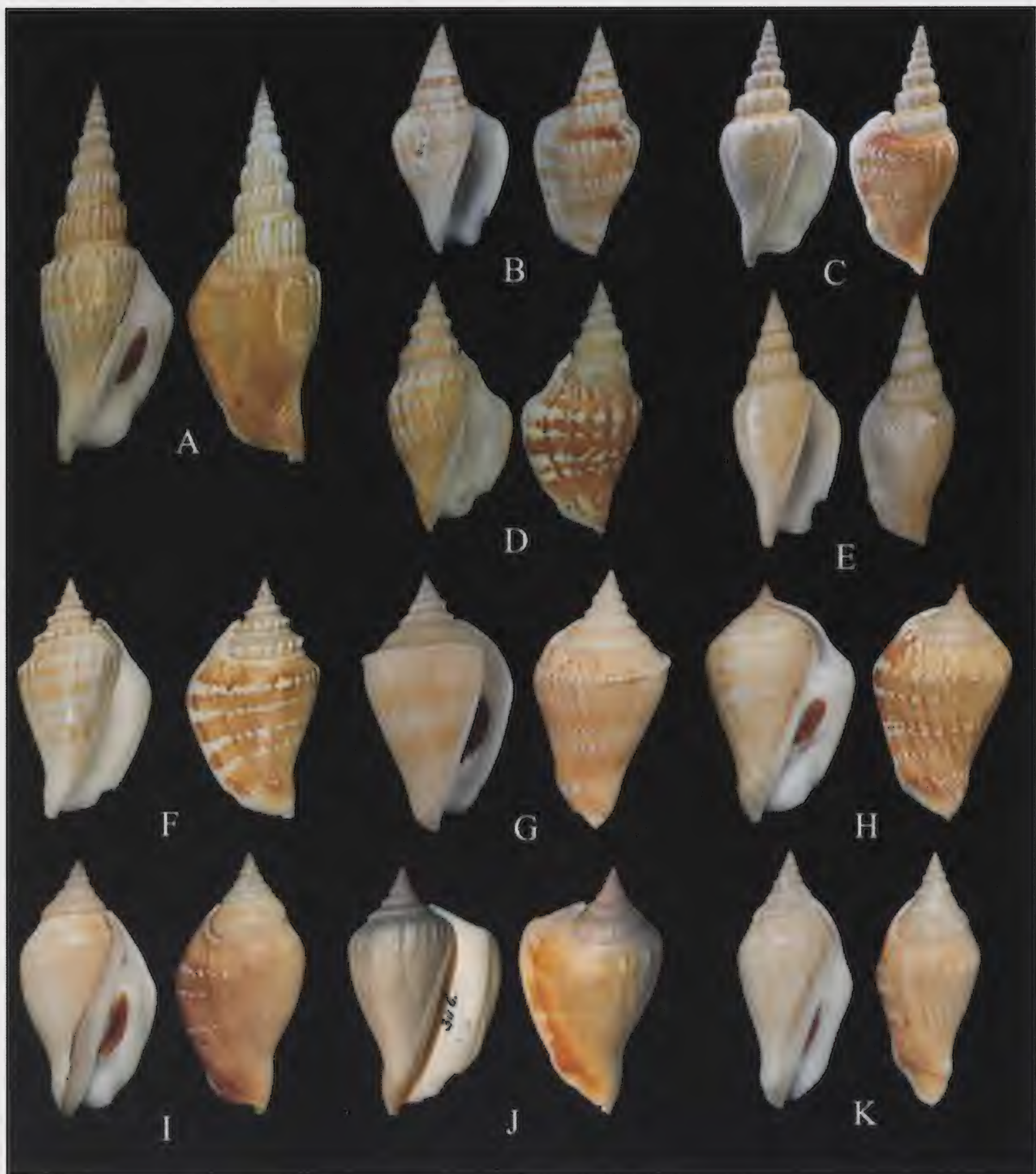
**Figure 1.** Morphological features used to determine character states - (1) The texture of aperture, (2) Uniformity sculptural shape of inner labrum, (3) Marginal fold, (4) Lip edge callous, (5) Texture of the columella, (6) Columella callosity prior to the formation of the anterior canal callosity, (7) The shape of the columella, (9) Posterior sinus lobes, (10) Shape of posterior sinus, (11) Both sides of sinus well developed, (12) Stromboidal notch and lobe, (13) Sculpture of the shield, (14) Acute ridge left side of shield, (15) Shape of shoulder, (16) Sculpture of the shoulder, (17) Shape of body whorl, (18) Flange fold, (19) Flange stepped at edge, (20) Cross sectional shape of flange, (21) Shoulder sculpture, (22) Penultimate whorl spiral sculpture, (23) Penultimate whorl axial sculpture.





**Figure 2.** The revised phylogeny of Dolomenini tribus nov with the most parsimonious trees: A) The results of the first cladistic analysis using the type species for each genera resulting in two monophyletic groups, the Dolomenina subtribus nov. and Doxandrina subtribus nov., and the demonstration that *Mirabilistrombus* and *Laevistrombus* fall outside the Dolomenini tribus nov.; B and C) the resolution of the internal content of each of the two trees identified in the first analysis using all species extant contained within them.





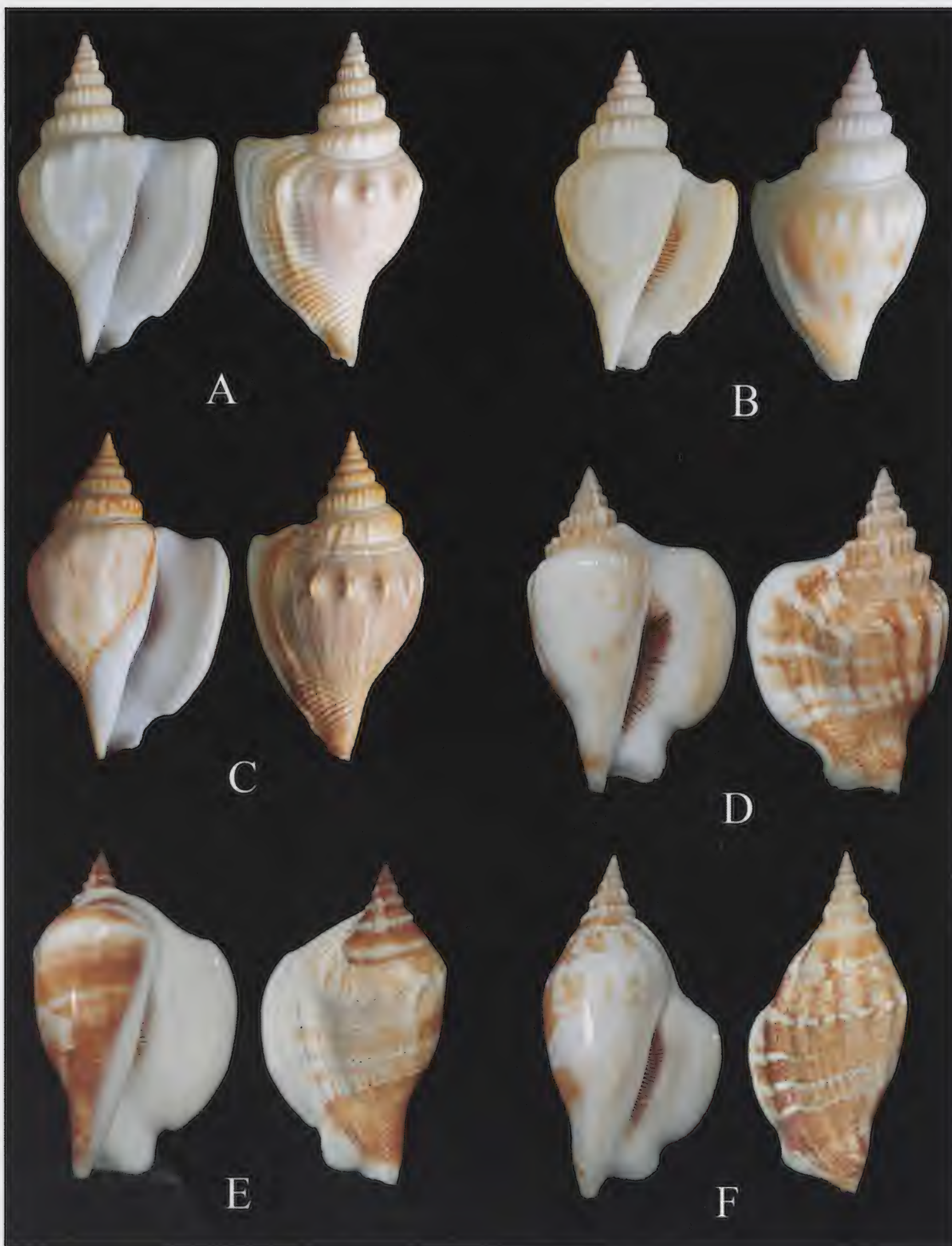
**Figure 3. Iconography of *Doxanderina subtribus* nov.:** *Doxander* Wenz, 1940 - A) *Doxander apicatus* (Man in't Veld and Visser, 1993), Quang Ngai, Vietnam, 92 mm, AMD STR0562; B) *Doxander campbelli* (Griffith and Pidgeon, 1834) Yirrkala, Gove, Northern Territory, Australia, 54 mm, SMC 13.026; C) *Doxander entropi* (Man in't Veld and Visser, 1993), Davao, Philippines, 82 mm, SMC 15.002; D) *Doxander japonicus* (Reeve, 1851), Honshu, Japan, 61 mm, AMD STR1058; E) *Doxander vittatus* (Linnaeus, 1758), Kurrumune Beach, Queensland, Australia, 61 mm, SMC 36.001. *Neodilatilabrum* Dekkers, 2008 – F) *Neodilatilabrum boucheti* (Thach, 2016) Khan Hoa Province, Vietnam, 45 mm, MNHN-IM-2000-30134 (= *Neodilatilabrum robustum* (Sowerby, 1875) fide Kronenberg *et al.* 2019). G) *Neodilatilabrum marginatum* (Linnaeus, 1758), Madras, India, 55 mm, SMC 66.002; H) *Neodilatilabrum sowerbyorum* (Visser and Man in 't Veld 2005), Okinawa, Japan, 48 mm, SMC 68.001; I) *Neodilatilabrum septimum* (Duclos, 1844), Balicasag Island, Philippines, 53 mm, SMC 69.002; J) *Neodilatilabrum simanoki* (Liverani, 2013), Sumatra, Indonesia, 54 mm, NCB-Naturalis RMNH MOL164040; K) *Neodilatilabrum succinctum* (Linnaeus, 1767), Madras, India, 53 mm, SMC 70.001.





**Figure 4. Iconography of *Dolomenina subtribus nov.*:** *Dolomena* Wenz, 1940 - A) *Dolomena columba* (Lamarck, 1822), Nacala Bay, Mozambique, 2010, 52 mm, SMC 60.001; B) *Dolomena hickeyi* (Willan, 2000), Dingo Beach, Queensland, 2006, 47 mm, SMC 57.001; C) *Dolomena pulchella* (Reeve, 1851), Cebu Island, Philippines, 1986, 33 mm, SMC 59.004. *Labiostrombus* Oostingh, 1925 - D) *Labiostrombus epidromis* (Linnaeus, 1771), Goeland Island, New Caledonia, 2015, 78 mm, SMC 40.008. *Ministrombus* Dekkers, 2008 - E) *Ministrombus athenius* (Duclos, 1844), Borneo, Indonesia, pre 1990, 34 mm, SMC 53.003; F) *Ministrombus minimus* (Linnaeus, 1771), Balicasag Island, Philippines, 2014, 33 mm, SMC 59.008; G) *Ministrombus variabilis* (Swainson, 1820), Dingal Island, Philippines, 2009, 55 mm, SMC 52.008. *Amabiliplicatus* gen. nov. - H) *Amabiliplicatus plicatus* (Röding, 1798), Egypt, Red Sea, 1962, 63 mm, SMC 61.003; I) *Amabiliplicatus sibbaldi* (Sowerby, 1842), Kerala, India, 2013, 36 mm, SMC 62.002; J) *Amabiliplicatus yerburyi* (Smith, 1891), trawled, Somalia, 2010, 45 mm, SMC 61.001.





**Figure 5. Iconography of *Dolomenina subtribus* nov.: *Dominus* gen. nov. - A) *Dominus abbotti* (Dekkers & Liverani, 2011), off Racha Island, Andaman Sea, 2005, 39 mm, SMC 65.001; B) *Dominus wienekei* (Wiersma & Monsecour, 2012), Rabaul, Papua New Guinea, 2000, 45 mm, SMC 64.001; C) *Dominus labiosus* (Wood, 1828), Tulear, Madagascar, 2010, 68 mm, SMC 63.001. *Pacificus* gen. nov. - D) *Pacificus dilatatus* (Swainson, 1821), Dingo Beach, Queensland, 2002, 40 mm, SMC 59.012; E) *Pacificus orosminus* (Duclos, 1844), Davao Island, Philippines, 2013, 53 mm, SMC 55.001; F) *Pacificus swainsoni* (Reeve, 1850), Vietnam, 2014, 71 mm, SMC 56.002.**



## A Review of the Genus *Morum* (Gastropoda: Harpidae) in the Western Atlantic, with the Description of Two New Species from Brazil

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**ABSTRACT** Seven species of the moruminine harpid genus *Morum* (*sensu stricto*) are now known to occur within the Tropical Western Atlantic Region, with three species being restricted to the Caribbean Molluscan Province and four species being restricted to the Brazilian Molluscan Province. The Caribbean Molluscan Province contains *Morum oniscus*, *M. purpureum*, and *M. strombiforme*, while the Brazilian Molluscan Province contains *M. bayeri*, *M. berschaueri*, and two new species, *Morum damasoi* n. sp. and *Morum mariaodeteae* n. sp., which are described here.

**KEY WORDS** *Morum*, *Morum damasoi*, *Morum mariaodeteae*, Moruminae, Harpidae, Tropical Western Atlantic Region, Caribbean Molluscan Province, Brazilian Molluscan Province, Brazil

### INTRODUCTION

The moruminine harpid genus *Morum* Röding, 1798 (*sensu stricto*) is widespread throughout the western Atlantic, ranging from Bermuda, southeastern Florida and the Florida Keys, south to southern Espírito Santo State, Brazil. Within this large biogeographical region, the *Morum* species are prominent members of their resident ecosystems and are classic indicators of shallow water tropical marine environments and coral reefs habitats. A recent comprehensive study on western Atlantic biogeography, undertaken by the senior author, has shown that this large region of tropical environments actually encompasses two molluscan faunal provinces; the Caribbean in the north and the Brazilian in the south (Petuch, 2013). The intervening Amazon River Delta acts as an ecological barrier to the molluscan faunas of the two provinces and has ensured the genetic isolation of the Caribbean and Brazilian faunas since at least the Pleistocene. Because of this, two separate and distinct *Morum* faunas have

evolved in the western Atlantic, with three species being known from the Caribbean Province and four species being known from the Brazilian Province.

Recently, the intrepid collector, explorer, and field worker, Damaso Monteiro, brought two new *Morum* species to our attention. These distinctive new harpids were collected in two relatively unexplored areas of Brazil; one from the coralline algal reefs of the northern coast, and one from the coral reef systems of the Abrolhos Platform along the south-central coast. These new species are described here and the known related Caribbean and Brazilian taxa are also discussed and illustrated as a baseline for comparison. Three other harpids are also present in the western Atlantic, but these are all members of the genus *Oniscidia* (= *Cancellomorum*) and will not be discussed in depth here along with the members of the genus *Morum sensu stricto*. The larger-shelled and more ornate genus *Oniscidia* is represented by the wide-ranging *Oniscidia dennisoni* (Reeve,



1842), which is found in both the Caribbean and Brazilian Provinces, by *Oniscidia lindae* (Petuch, 1987), which is confined to northern Colombia in the Caribbean Province, and by *Oniscidia matthewsi* (Emerson, 1967), which is confined to the northern part of the Brazilian Province.

The holotypes of the new *Morum* species are deposited in the molluscan collections of the Zoological Museum of the University of São Paulo and bear MZSP numbers. The known western Atlantic members of the harpid genus *Morum* are described below.

## SYSTEMATICS

Class: Gastropoda

Subclass: Orthogastropoda

Superorder: Caenogastropoda

Order: Sorbeoconcha

Infraorder: Neogastropoda

Superfamily: Volutoidea

Family: Harpidae

Subfamily: Moruminae

Genus: *Morum* Röding, 1798

**Diagnosis.** Shells small for family and subfamily, roughly cone-shaped, with flattened or only slightly elevated spires; shells ornamented with variable numbers of low, rounded knobs, always arranged in spiral rows around the body whorl; apertures proportionally narrow, bordered by wide parietal shields along columellar side and by strong teeth along edge of labrum; parietal shields variable in color, ranging from white and pink to dark rose-violet, ornamented with very numerous small pustules.

**Discussion.** A survey of the genus *Morum* (*sensu stricto*) in the western Atlantic (taken from Petuch, 2013) has shown that there are two separate species complexes within the region, with each complex being confined to a separate molluscan faunal province. The Caribbean

Province (Bermuda and the Bahamas, south to Suriname) is now known to house a complex of three species, including *Morum oniscus* (Linnaeus, 1767), *Morum purpureum* Röding, 1798, and *Morum strombiforme* (Reeve, 1842). The Brazilian Province (the Amazon River mouth south to Cabo Frio, Rio de Janeiro State) houses a complex of four species, including *Morum bayeri* Petuch, 2001, *Morum berschaueri* Petuch and Myers, 2015, and two previously undescribed species, here named *Morum damasoi* and *Morum mariaodeteae*. These seven western Atlantic species, along with the three western Atlantic *Oniscidia* species, altogether, represent the largest fauna of the Harpidae known from any single biogeographical region in the Atlantic and Eastern Pacific Oceans. The known species of western Atlantic morumine harpids are listed here by their resident biogeographical provinces.

## CARIBBEAN MOLLUSCAN PROVINCE SPECIES

*Morum oniscus* (Linnaeus, 1767)  
(Figure 1A, B)

**Synonyms.** *Cypraea conoidea* Scopoli, 1786; *Oniscia quadriseriata* Menke, 1830; *Oniscia triseriata* Menke, 1830. This species was originally named in the genus *Strombus*.

**Diagnosis.** Shell of average size for genus, roughly cone-shaped, with flattened spire; shoulder sharply-angled, slightly rounded, bordered with 8-10 knobs; body whorl ornamented with 4 widely-spaced rows of large rounded knobs, with one below shoulder, one around mid-body, one around anterior end, and one small row around base of siphonal canal; parietal shield proportionally large, well-developed, adherent, extending over at least half of shell base; parietal shield covered with very numerous tiny rounded pustules; labrum



thickened, smooth, with inner edge being lined by 12-14 large teeth; shell color white, covered with numerous dark brown speckles and small flammules, with largest and darkest flammules being on spire whorls; aperture and parietal shield pure white; protoconch white, projecting and mammilate, composed of 3 whorls.

**Distribution.** This small harpid ranges from Bermuda to southeastern Florida (Palm Beach County) and the Florida Keys, throughout the Bahamas and the entire Caribbean Sea Basin, south to the Lesser Antilles and Barbados. The species is absent from the Gulf of Mexico. The presence of *Morum oniscus* in southern Florida represents the only occurrence of this species in the Carolinian Molluscan Province (see Petuch, 2013).

**Discussion.** *Morum oniscus* is the most frequently-encountered moruminine harpid in the Caribbean region, being a well-known resident of most shallow water coral reef areas from Palm Beach County, Florida to Barbados. The species has been found to be especially common in the northern Caribbean and the Bahamas, and is abundant on outer islands such as the Abacos and Eleuthera. Farther south in the Caribbean area, *Morum oniscus* is less common, possibly due to competition with its sympatric congeners *M. purpureum* and *M. strombiforme*.

*Morum purpureum* Röding, 1798  
(Figure 1E, F, G)

**Synonym.** *Oniscia lamarcki* Deshayes, 1844

**Diagnosis.** Shell of average size for genus, roughly cone-shaped, with a flattened spire; shoulder sharply-angled, bordered by 8-9 large, rounded knobs; body whorl ornamented with 3 widely-spaced rows of large rounded knobs, with one below shoulder, one around mid-body,

and one around anterior end; parietal shield proportionally large, well-developed, adherent, extending over at least half of shell base; parietal shield covered with very numerous tiny rounded pustules; labrum thickened, smooth, with inner edge being lined by 10-12 very large teeth; shell color pale tan to dark brown, covered with numerous large dark brown patches and flammules; spire whorls colored dark brown; parietal shield and labrum bright pink or deep rose-purple; protoconch pale tan, projecting and mammilate, composed of 3 whorls.

**Distribution.** The range of the species is known to extend from southeastern Florida (Palm Beach County), southward across the Bahamas Platforms, the entire Antillean Arc, throughout the entire Caribbean Sea Basin, and southward to Barbados. The species is absent from the Gulf of Mexico and from the island of Bermuda.

**Discussion.** As “*Morum oniscus purpureum*”, this taxon is the type species of the genus *Morum*. Although originally considered to be a form or subspecies of the common, widespread *M. oniscus*, *M. purpureum* can be seen to be morphologically distinct, having stronger, better-developed, and proportionally-smaller dorsal knobs, in having only three rows of knobs and not four rows as in *M. oniscus*, and in being a much more colorful shell, with dark brown spire whorls and a bright pinkish-lavender or purple parietal shield and labrum. *Morum purpureum* has a range similar to that of *M. oniscus*, but is most frequently-encountered in the southeastern Caribbean area, primarily on the Dutch Caribbean Islands of Aruba, Bonaire, and Curaçao. Very dark specimens, with intense purple parietal shields, are known from Martinique and Guadeloupe Islands.



*Morum strombiforme* (Reeve, 1842)  
(Figure 1C, D)

**Diagnosis.** Shell of average size for genus, roughly cone-shaped, with elevated spire and sloping spire whorls; shoulder sharply-angled, slightly rounded, bordered with 8-10 knobs; body whorl ornamented with 4 widely-spaced rows of large rounded knobs, with one below shoulder, one around mid-body, one around anterior end, and one small row around base of siphonal canal; rows of knobs and intercalated areas ornamented with 8-10 large, raised spiral cords; parietal shield proportionally large, well-developed, adherent, extending over at least half of shell base; parietal shield covered with very numerous tiny rounded pustules; labrum thickened, smooth, with inner edge being lined by 12-14 large teeth; shell color dirty white or pale tan, covered with very numerous dark brown speckles and small flammules, with largest and darkest flammules being on spire whorls; spiral cords of body whorl marked with evenly-spaced dark brown or blackish-brown dots, giving shell a heavily mottled appearance; aperture and parietal shield pure white; protoconch white, projecting and mammilate, composed of 3 whorls.

**Distribution.** The range of *Morum strombiforme* extends from the eastern half of the Yucatan Peninsula of Mexico, eastward along the coasts of Honduras, Nicaragua, Costa Rica, and Panama, and also throughout the Greater Antilles and the Virgin Islands. The species is most frequently collected along the coast of Honduras and the Bay Islands of Roatan, Guanaja, and Utila. Records of *Morum strombiforme* from Brazil are based on misidentified specimens of *M. bayeri* and *M. berschaueri* and the species does not occur within the Brazilian Province.

**Discussion.** This uncommon species has a smaller range than does its closely-related congener, *Morum oniscus*, being most frequently-encountered in the western Caribbean region, from eastern Quintana Roo and Belize to Honduras. *Morum strombiforme* differs from *M. oniscus* in being a larger and more elongated shell with a much higher and more protracted spire and in having distinctly sloping spire whorls. *Morum strombiforme* is also a much more heavily-sculptured shell, being ornamented with numerous very strong, raised spiral cords that overlap onto the rows of rounded knobs, giving the shell a rougher appearance. While *Morum oniscus* is generally a pale-colored or white shell with scattered tiny brown dots, *Morum strombiforme* is consistently a much darker-colored shell, being covered with dense clumps of large dark brown or black dots and large amorphous dark brown flammules. In this last character, *M. strombiforme* somewhat resembles the dark-colored *M. bayeri* from Brazil, leading to the erroneous assumption that this species was also present in the Brazilian Province (discussed next).

**BRAZILIAN MOLLUSCAN  
PROVINCE SPECIES**

*Morum bayeri* Petuch, 2001  
(Figure 2A, B)

**Diagnosis.** Shell of average size for genus, roughly cone-shaped, with slightly elevated spire and sloping spire whorls; rounded, bordered with 10-12 low, undulating knobs; body whorl ornamented with 4 widely-spaced rows of large rounded knobs, with one below shoulder, one around mid-body, and one around anterior end; rows of knobs and intercalated areas ornamented with numerous fine, raised spiral cords and faint grooves, giving shell a rough appearance; parietal shield proportionally



large, well-developed, adherent, extending over at least half of shell base; parietal shield covered with very numerous tiny rounded pustules; labrum thickened, smooth, with inner edge being lined by 16-18 large, elongated teeth that extend onto the base of the labrum; shell color variable, being pale yellow-tan or dark ochre yellow, densely covered with numerous large black amorphous flammules, dots, and blotches, mostly concentrated in areas between rows of knobs; flammules, extend onto spire whorls; aperture and parietal shield pure white; protoconch pale yellow-tan, projecting and mammilate, composed of 3 whorls.

**Distribution.** The range of the species is known to extend around the “nose” of Brazil, occurring in the States of Rio Grande do Norte, Paraibo, Pernambuco, Alagoas, and Sergipe. The species may also extend along northern Bahia State, but records from there need confirmation.

**Discussion.** Because of its dark-colored shell and slightly raised spire whorls, the Brazilian *Morum bayeri* has often been confused with the western Caribbean *M. strombiforme* (Figure 1E, F). The Brazilian endemic species differs from its Caribbean congener in having a stockier, more truncated, and more rounded shell outline, in having lower and less-elevated spire whorls, in having a much darker shell color, being yellow with large black flammules, and in having more numerous and better-developed labral teeth, which extend across the entire base of the labrum. Some specimens of *M. bayeri*, such as the holotype, are mostly a deep yellow-ochre color with only scattered black speckles and flammules while others are almost entirely black.

*Morum berschaueri* Petuch & Myers, 2015  
(Figure 2C, D)

**Diagnosis.** Shell of large for genus, averaging 35 mm, roughly cone-shaped, with slightly elevated spire and stepped spire whorls; shoulder sharply-angled, slightly bordered with 10-11 large, prominent, pointed knobs; body whorl ornamented with 3 widely-spaced rows of large rounded knobs, with one below shoulder, one around mid-body, one around anterior end; rows of knobs and intercalated areas ornamented with numerous large, undulating, raised spiral cords, giving shell a rough appearance; parietal shield proportionally large, well-developed, adherent, extending over at least half of shell base; parietal shield covered with very numerous tiny rounded pustules; labrum thickened, smooth and shiny, with inner edge being lined by 12-14 proportionally-small teeth; shell color dirty white or pale yellow-white, covered with very numerous dark tan speckles, primarily on rows of large knobs, on large spiral cords, and on suture of spire whorls; aperture and parietal shield pure white; protoconch white, projecting and mammilate, composed of 3 whorls.

**Distribution.** Confirmed records of this rare shell are known only from the southern half of Espirito Santo State, Brazil, particularly in the Guarapari area. The species may extend southward into northern Rio de Janeiro State. A dwarf form, measuring only around 19 mm in length, has been collected in northern Espirito Santo State and southernmost Bahia State. Further study may show that this represents yet another new species of Brazilian *Morum*.

**Discussion.** *Morum berschaueri* is the largest-known member of its genus, being almost twice as large as *M. oniscus* and one-third larger than the next largest species, *M. strombiforme*. Besides its size, *M. berschaueri* differs from its



congeners in having pointed shoulder knobs that project posteriorward and produce a distinct coronated effect.

*Morum damasoi* Petuch & Berschauer, new subspecies  
(Figures 2E, F; 3E, F)

**Description.** Shell small for genus, averaging only 17.5 mm, distinctly cone-shaped, with straight sides and flattened spire whorls; shoulder sharply-angled, bordered with 9-10 small, sharp knobs; body whorl ornamented with 8 large, evenly-spaced spiral cords, with cord around anterior end being largest best-developed; large spiral cords ornamented with 8-10 small, rounded beads, giving shell surface a pebbled appearance; areas between cords heavily ornamented with numerous fine raised spiral threads; parietal shield proportionally large, well-developed, adherent, extending over at least half of shell base; parietal shield covered with very numerous tiny rounded pustules; labrum thickened, smooth, with inner edge being lined by 18-20 small teeth; shell color yellow-white, covered with very numerous black dots, speckles, and small flammules, with largest and darkest flammules being on spire whorls; black flammules arranged in longitudinal rows and often encircle rounded beads on spiral cords; aperture and parietal shield white; protoconch pale yellow, projecting and mammilate, composed of 3 whorls.

**Type Material.** HOLOTYPE -- length 17.5 mm, width 11.5 mm, 20 m depth off Coroa Vermelha, Abrolhos Platform, Brazil, MZSP 150893; OTHER MATERIAL EXAMINED -- length 18 mm, width 12 mm, from the same locality and depth as the holotype, in the research collection of the senior author; length 18 mm, from the same locality and depth as the holotype, in the Damaso Monteiro collection.

**Type Locality.** 20 m depth in coral rubble, off Coroa Vermelha, Abrolhos Platform, southern Bahia State, Brazil.

**Distribution.** Known only from coral reef areas on the Abrolhos Platform off southern Bahia State, south central Brazil.

**Etymology.** Named for Damaso Monteiro of Fortaleza, Brazil and Oporto, Portugal, who discovered this new species, and the following species, while exploring the northern and central coasts of Brazil. The taxon honors his many important contributions to Brazilian malacology.

**Discussion.** *Morum damasoi* is the smallest of the known western Atlantic *Morum* species and is less than half the length of its Brazilian congener, *M. berschaueri*. This new species also differs from the other six western Atlantic species in being the only one that lacks the three or four rows of large knobs on the body whorl, having instead eight large beaded cords that encircle the shell. This character, along with the flat spire and sharply-edged shoulder, readily separate *M. damasoi* from any other known *Morum* species.

*Morum mariaodeteae* Petuch & Berschauer, new subspecies  
(Figures 3A, B; 3C, D)

**Description.** Shell small for genus, averaging only 18 mm, oval in shape, with rounded sides; spire only slightly elevated; shoulder rounded, bordered with 10-11 low, flattened knobs; body whorl ornamented with 4 widely-spaced rows of large rounded knobs, with one along shoulder, one below shoulder, one around mid-body, and one around anterior end; rows of knobs and intercalated areas heavily ornamented with numerous strong raised spiral cords and threads; parietal shield proportionally large, well-



developed, adherent, extending over at least half of shell base; parietal shield white or pale pinkish-white, covered with very numerous fine rounded pustules; labrum thickened, smooth, with inner edge being lined by 15-16 small teeth, which often extend onto base of labrum; shell color pale cream-tan, covered with very numerous light brown and tan speckles and large dark brown flammules, which often arranged in longitudinal zebra-striped pattern; protoconch pink, projecting and mammilate, composed of 3 whorls.

**Type Material.** HOLOTYPE -- 18.5 mm, width 12 mm, in rock rubble off Camocim, Ceará State, Brazil, MZSP 150894; OTHER MATERIAL EXAMINED -- length 19 mm, from the same locality and depth as the holotype, in the research collection of the senior author; length 18 mm, from the same locality and depth as the holotype, in the research collection of the junior author; length 19 mm, from the same locality and depth as the holotype, in the Damaso Monteiro collection.

**Type Locality.** In coralline algal rubble, 35 m depth off Camocim, Ceará State, Brazil.

**Distribution.** Known only from coralline algal reefs along the States of Maranhao, Piaui, and Ceará, northern Brazil.

**Etymology.** Named for Maria Odete Monteiro of Oporto, Portugal, mother of Damaso Monteiro.

**Discussion.** Of the known northern Brazilian *Morum* species, *M. mariaodeteae* most closely resembles *M. bayeri* from northeastern Brazil, but differs in having a smaller shell with a more rounded profile, in being a lighter-colored shell that lacks any black mottling, in having light brown zebra-patterned longitudinal flammules, in having proportionally-larger and better-produced rows of knobs on the body whorl, and in having a proportionally-larger protoconch with a distinctive pink color.

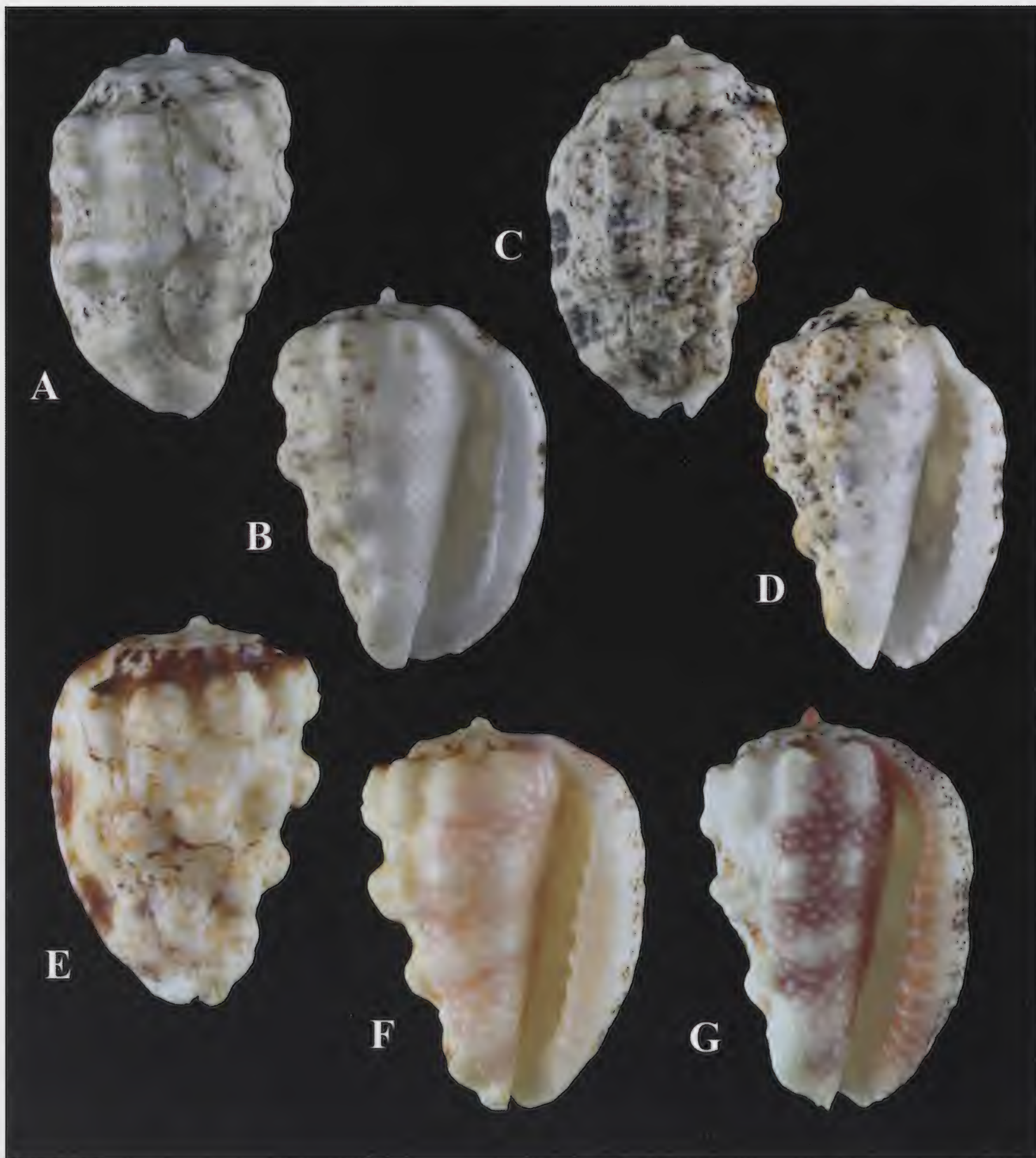
## ACKNOWLEDGMENTS

We thank Damaso Monteiro, of Fortaleza, Brazil and Oporto, Portugal for the generous donation of the type specimens of the two new species. We also thank Luis Vela, Merida, Yucatan, Mexico, Director of the Museo del Mar, for the generous donation of the *Morum strombiforme* illustrated in this paper.

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**Figure 1. *Morum* Species from the Caribbean Molluscan Province.**

A, B = *Morum oniscus* (Linnaeus, 1758), length 25 mm, in sand and coral rubble, 1 m depth off Cape Eleuthera, Eleuthera Island, Exuma Sound, Bahamas; C, D = *Morum strombiforme* (Reeve, 1842), length 28 mm, found fresh dead on the beach, Playa del Carmen, Quintana Roo State, eastern Yucatan Peninsula, Mexico; E, F = *Morum purpureum* Röding, 1798, length 23 mm, under coral rubble, 2 m depth off Malmok, Aruba (*Morum lamarcki* (Deshayes, 1844) is a synonym); G = *Morum purpureum* Röding, 1798, length 24 mm, under coral rubble, 9-12 m, Curaçao.

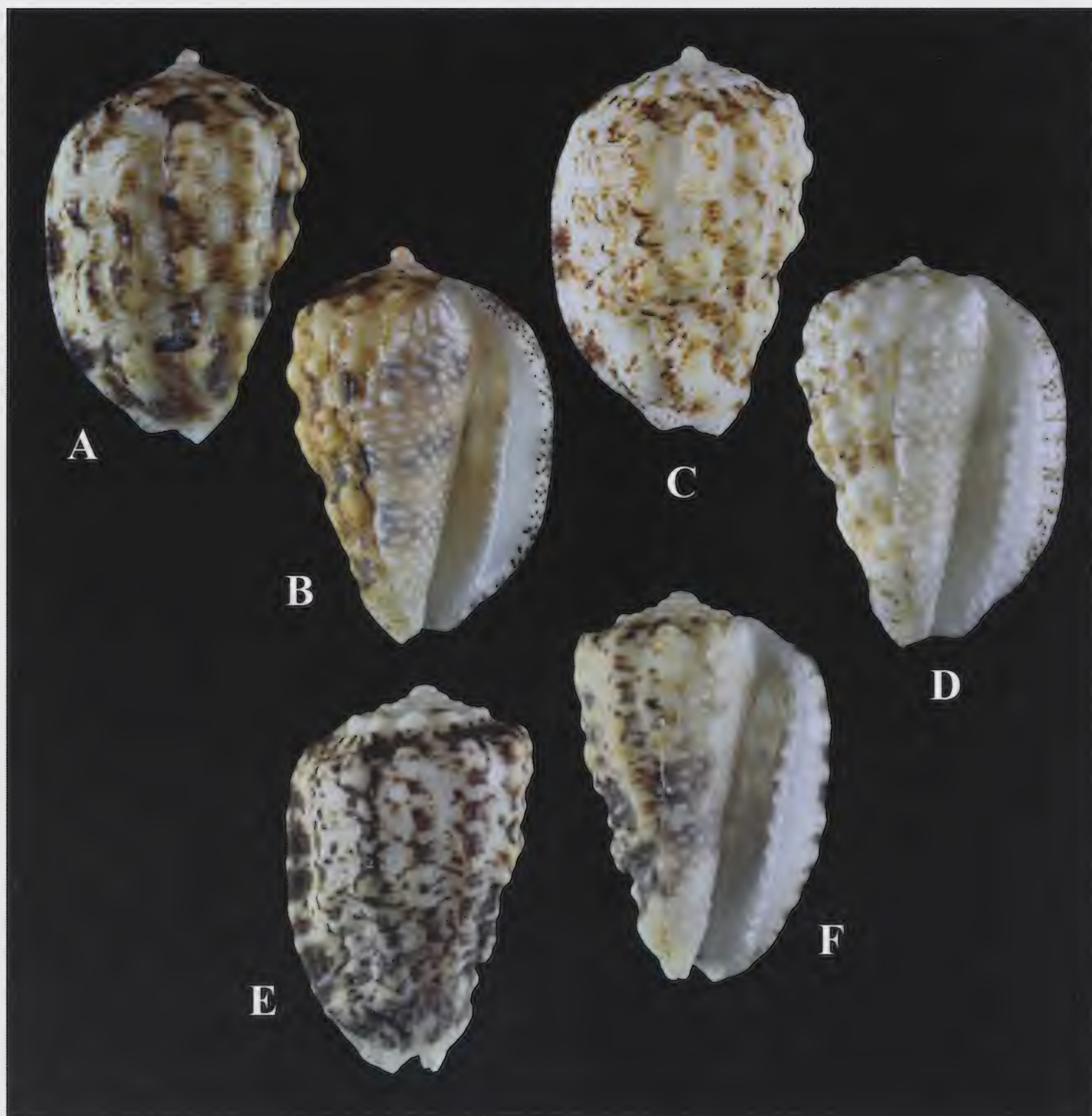




**Figure 2. *Morum* Species from the Brazilian Molluscan Province.**

**A, B** = *Morum bayeri* Petuch, 2001, length 23 mm, in coralline algae, 3 m depth off Rio do Fogo, Rio Grande do Norte State, Brazil; **C, D** = *Morum berschaueri* Petuch and Myers, 2015, length 36 mm, dredged from 20 m depth in the Guarapari Channel, Guarapari, Espírito Santo State, Brazil; **E, F** = *Morum damasoi* Petuch and Berschauer, new species, holotype, length 17.5 mm, in coral rubble, 20 m depth off Coroa Vermelha, Abrolhos Platform, southern Bahia State, Brazil.





**Figure 3. New *Morum* Species from the Brazilian Molluscan Province.**

A, B = *Morum mariaodeteae* Petuch and Berschauer, new species, holotype, length 18.5 mm, found in coralline algal rubble, 35 m depth off Camocim, Ceará State, Brazil; C, D = *Morum mariaodeteae* Petuch and Berschauer, new species, length 18 mm, in coralline algal rubble, 35 m depth off Camocim, Ceará State, Brazil (Berschauer Collection); E, F = *Morum damasoi* Petuch and Berschauer, new species, length 18 mm, in coral rubble, 20 m depth off Coroa Vermelha, Abrolhos Platform, southern Bahia State, Brazil (Petuch Collection).



## Descriptions three rare and little known of *Neptunea* (Gastropoda; Buccinidae) from the Eastern Bering Sea slope, one new to science

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**ABSTRACT** Three rare and little known species of the genus *Neptunea* Röding, 1798 from continental slope of the eastern Bering Sea are discussed. The rediscovery of the enigmatic *Neptunea insularis* (Dall, 1895), a range extension for *Neptunea alabaster* Alexeyev & Fraussen, 2005, and a new species, unique amongst *Neptunea* in having five cusps on the lateral teeth, of the radula, opposed to three found in nearly all other *Neptunea*. The three species are described herein and their distributions defined.

**KEY WORDS** Bering Sea, *Neptunea*, *Neptunea insularis*, *Neptunea alabaster*, *Neptunea mcleani*, Alaska, gastropod, biodiversity

### INTRODUCTION

The genus *Neptunea* in the North Pacific area is very large and diverse and a number of complexes have yet to be worked out. Fraussen & Terry, 2007 reviewed the genus in “A Conchological Iconography” and illustrated several as yet undescribed species from the region, mostly from the western Bering Sea. The mollusk fauna of the bathyal depths of the eastern Bering Sea is poorly known and includes numerous species of *Neptunea*, many of them undescribed. In 2010, while participating on a National Marine Fisheries resource assessment survey numerous specimens of the genus *Neptunea* were taken at depths ranging from 200-1200 m. Along with the recognized *N. pribiloffensis* (Dall, 1919), *N. amianta* (Dall, 1890), and *N. aleyxyevi* Fraussen & Terry, 2007, the enigmatic *N. insularis* (Dall, 1895) was rediscovered, as well as specimens of several undescribed species, including four specimens of an unusual, weakly ribbed, uniformly white shelled species. Two years later,

in 2012 Dr. Duane Stevenson (NMFS) recovered a specimen of *Neptunea alabaster* Alexeyev & Fraussen, 2005 from Pervenets Submarine Canyon on a subsequent survey.

### Abbreviations

NMFS - National Marine Fisheries Service

NOAA - National Oceanic and Atmospheric Administration

LACM - Los Angeles County Museum of Natural History

SBMNH - Santa Barbara Museum of Natural History

ZMMU - Zoological Museum Moscow State University

### SYSTEMATICS

Superfamily: Buccinoidea Rafinesque, 1815

Family: Buccinidae Rafinesque, 1815

Subfamily: Colinae Gray, 1857

Genus: *Neptunea* Röding, 1798

Type species: “*Murex*” *antiquus* Linnaeus, 1798 (by subsequent designation)



*Neptunea insularis* (Dall, 1895)  
(Figures 1A-G)

**Type locality.** Bering Sea, near Pribilof Islands, 336 m. Albatross station 3489 (57° N, 173°).

**Type.** USNM 107000. (Figure 1A), illustrated by Kosuge (1972).

**Material studied.** Type, USNM 10700; 1, SBMNH 169023, 128.4 mm. Zhemchug Canyon (58°17.41 N, 175°05.32 W), 642 m. (NMFS 94-201001-72); 1, SBMNH 169023, 102.3 mm. S of Zhemchug Canyon (57°08.34 N, 173°57.05 W), 638 mm. (NMFS 94-201001-4); 1, RNC 4145, 123.7 mm. Zhemchug Canyon (58°20.56 N, 175°04.21 W), 574 m. (NMFS 94-201001-73); 2, LACM 182155, 99.0 & 90.8 mm. NW of Pribilof Canyon (56°30.75 N, 172°22.42 W), 616 m. (94-201001-97); 2, RNC 4146, 127.5 & 97.2 mm. NW of Pribilof Canyon (56°29.62 N, 171°57.08 W), 519 m. (NMFS 94-201001-100); 2, RNC 4147, 116.7 & 95.1 mm. Bering Canyon, N of Akutan Island, Aleutian Is. (54°27.51 N, 165°56.31 W), 505 m. (94-201001-197); 1, RNC 4148, 131.2 mm. SE of Pervenets Canyon (58°37.02 N, 175°07.62 W), 410 m. (NMFS 94-201001-11); 2, RNC 4672, 147.4 & 127.3 mm. Zhemchug Canyon (58°20.46 N, 174°16.86 W), 175 m. (NMFS 89-201201-168).

**Description.** “Shell large, solid, rather thin, with about six whorls (excluding the nucleus); whorls full, rounded, slightly excavated in front of the appressed suture; (spiral) sculpture (see Figure 1E) of, on the last whorl, three sizes of flattish, rounded threads, alternating regularly in size, but on the upper whorls of only two sizes separated only by shallow grooves; transverse (axial) of moderately prominent incremental lines; aperture ample, the pillar lip blotched with livid pink and white, the pillar twisted, with a solid white inner edge and strong

siphonal fasciole; canal moderate, slightly recurved; outer lip slightly crenulated by the sculpture, sharp, very slightly expanded; throat smooth, pinkish; epidermis (periostracum) very thin and translucent, closely adherent to the surface; operculum normal, light brown. Length of shell 100 mm; max. diameter 56 mm. (after Dall, 1895).” (from Oldroyd, 1927) (Emphasis added)

**Color.** Pink to pale tan, primary spiral cords often darker. Radula (Figure 1G): Rachidean tooth very broad and short, with three short, stout triangular cusps of equal size. Lateral teeth stout, with three cusps, the outer cusp thick, curved, almost twice as long as middle and inner cusps, which are subequal in length.

**Distribution.** Eastern Bering Sea, along the upper continental slope, from SE of Pervenets Canyon south to Bering Canyon, N of Akutan Island, at depths of 175-638 m, but typically below 400 m.

**Habitat.** Found on mud bottoms with a bottom temperature of 2.6°C to 3.6°C.

**Remarks.** The nucleus of this species (Figure 1F) is about 4.5 mm in diameter, and early whorls have two faint cords. Specimens illustrated by Koen & Terryn, 2007, and Kantor & Syseov, 2007 are mis-identifications. Higuchi, 2006 illustrated something identified as this species from off Hokkaido Island, Japan, but it's relationship to *N. insularis* remains unclear.

*Neptunea alabaster* Alexeyev & Fraussen, 2007  
(Figure 1H)

**Type locality.** Bering Sea (59°06.41 N, 166°02.7 E), 330-335 m.

**Type.** ZMMU Lc-25896



**Description.** Shell of medium size (to 120 mm), thin but solid, snow-white. Subsutural slope broad, concave on upper spire whorls, straight or slightly convex on body whorl. Upper spire whorls sculptured with two sharp primary spiral cords, penultimate whorl with four strong primary cords, the fourth one occasionally partly concealed under lower suture, interspaces with alternating broad and finer secondary spiral cords. Outer lip thin, flared, irregular (after Fraussen & Terryn, 2007). Radula (Figure 1I): Rachidean tooth broad and tall, excavated medially, bearing three subequal cusps. Lateral teeth with 3/4 cusps, outer cusp large thick, strongly curved, inner cusp straight, much smaller than outer one, in cusps about half as long as inner cusp. Examined specimen is unusual in that the laterals on one side have two subequal central cusps, the laterals on the other side have only a single cusp. It is unknown which is the usual number for this species.

**New Record.** A single specimen, RNC 4969 (Figure 1H), 74.0 mm. Pervenets Canyon (59°35.17 N, 178°24.78 W), 913 m. (NMFS 94-201201-33). Bottom temperature 3.1°C. (*Leg.* Dr. Duane E. Stevenson, June 2012.) Extends the known range of this species about 660 km east, into the Eastern Bering Sea. It also extends the bathymetric range from 440 m to 913 m.

**Distribution.** Bering Sea, Gulf of Oljuter, Russia (169°45 E) to Pervenets Sea Canyon, Alaska (178°24 W), at 180-913 m.

*Neptunea mcleani* Clark, new species  
(Figures 2A-H)

**Type locality.** Alaska, Bering Sea, North side of Bering Submarine Canyon (54°16.72 N, 167°44.31 W), 1018 m. (*Leg.* R. Clark, 11 July 2010) (NMFS 94-201001-161).

**Type material.** Holotype, LACM 3663 (Figure 2A), 106.8 mm; Paratype 1, SBMNH 169022, 95.7 mm. Bering Sea, Bering Submarine Canyon (54°48.1 N, 167°40.45 W), 1065 m. (NMFS 94-201001-143); Paratype 2, RNC 5050, 107.3 mm. Bering Sea, NW of Zhemchug Submarine Canyon (58°37.85 N, 177°47.04 W), 818 m.

**Referred material.** 1, RNC 5051, 129.1 mm. Bering Sea, North of Unalaska Island, South side of Bering Submarine Canyon (55°13.53 N, 167°53.4 W), 414 m. Differs from typical specimens in bearing six low varices on the outer portion of the body whorl.

**Diagnosis.** Shell relatively large, broad, fusiform, with 4-5 rounded whorls, suture impressed; spire with four moderately heavy, rounded spiral cords (7-8 on body whorl), with a single smaller, lower secondary cord, and often 2-4 fine spiral lirae between, crossed by numerous fine growth lines; aperture large, about half of shell height, canal moderately long. Shell white with very thin green/tan periostracum.

**Description.** Shell moderately large (to 10 cm+), broad, relatively thin, fusiform, with 5 (possibly 6) rounded whorls, suture strongly impressed, apex eroded, aperture large, about one half of shell height, outer lip not flaring; axial sculpture of very numerous, fine growth lines; spiral sculpture of narrow, widely spaced, rounded ribs (Figure 2B), four on penultimate whorl, seven to eight on body whorl, with a single smaller, lower rib and 2-4 fine lire on the interspaces, sub-sutural slope with two cords; canal short, only slightly curved, outer lip slightly flared. Color, uniformly white. Radula (Figure 2F): Rachidean tooth chevron shaped, with (normally) two small (often splitting), triangular cusps. Lateral teeth with five sharply pointed cusps, distal cusp large, curved, nearly



twice as long as proximally most cusp. Inner four cusps grading distally from the proximal cusp, distal most of these smaller cusps about half as long as proximal most cusp. What appears to be the egg capsules (Figures 2G, H) of this species were taken at station 94-2010-01-143. Capsules are yellow, triangular, attached by a short stalk at one corner, about 15 mm x 10 mm, sculptured with irregular crisscrossing ribs forming diamond-shaped reticulations.

**Distribution.** Alaska, Eastern Bering Sea continental slope, from W of Zhemchug Submarine Canyon (58°37' N) south to Bering Submarine Canyon (54°16' N), at depths of 412 to 1065 m.

**Habitat.** Occurs on soft mud bottoms, at temperatures of 2.7°C to 3.7°C.

**Remarks.** *Neptunea mcleani* resembles *Neptunea pribiloffensis* (Dall, 1919), but differs in having a taller, more slender profile, more pronounced spiral ribs, and lacks the angulation at the shoulder. *Neptunea mcleani* is unique amongst *Neptunea*, in having five cusps on the lateral teeth. Only two other species of *Neptunea* are known to have more than three. *Neptunea costaria* Fraussen & Terryn, 2007 has seven cusps, and an as yet undescribed species from the Aleutian Islands has four (McLean & Clark, in prep.). The one radula of *N. alabaster* examined was abnormal, having four cusps on one side, and three on the other, so it is uncertain which is the normal count for that species.

**Etymology.** The name honors my friend and mentor the late Dr. James H. McLean, formerly of the Los Angeles County Museum of Natural History. Before his untimely death in 2015, Dr. McLean was in the process of reviewing the *Neptunea* (and other Buccinidae) in the North Pacific.

## ACKNOWLEDGEMENTS

I am grateful to Dr. Garold Hoff, NOAA/NMFS, for the opportunity to participate on the NMFS Bering Sea slope survey and for providing the distribution map; Dr. Duane Stevenson, NOAA/NMFS for retaining the specimen of *Neptunea alabaster* Dr. James Orr and Robert Lauth, NOAA/NMFS for providing data; for assistance at their respective institutions, Dr. Jann Vendetti and Lindsey Groves, LACM; Dr. Henry Chaney and Dr. Daniel Geiger, SBMNH (the latter for imaging the radula); the captain and crew of the R/V Vesteraalen. Finally, the reviews of two anonymous reviewers was invaluable.

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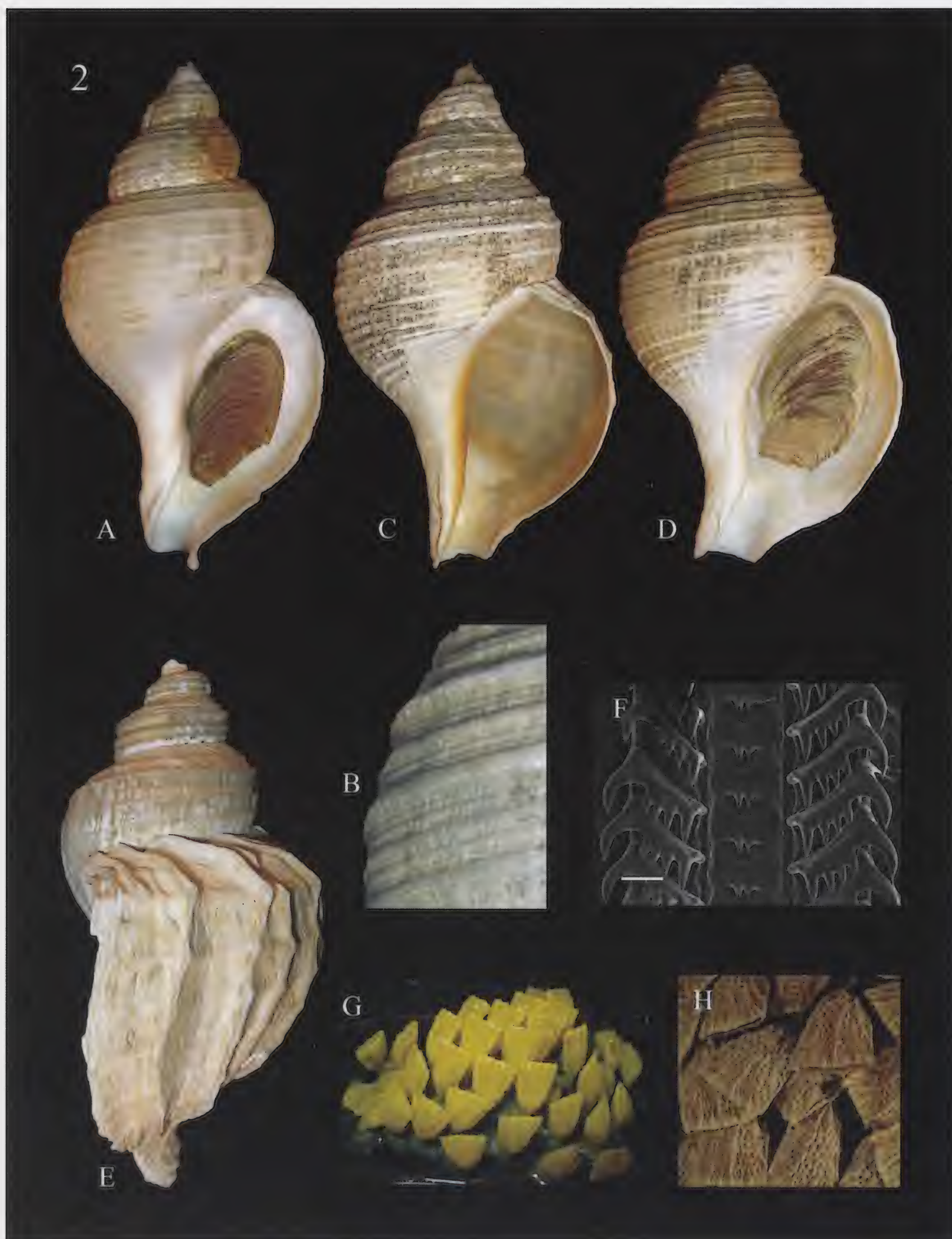
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**Figure 1.** *Neptunea insularis*. **A** = Holotype, USNM 107000; **B** = RNC 4148, Zhemchug Canyon, 410 m, 131.2 mm; **C** = RNC 4672, Zhemchug Canyon, 175 m, 147.4 mm; **D** = SBMNH 169023, Zhemchug Canyon, 642 m, 128.4 mm; **E** = RNC 4672, close-up of sculpture; **F** = RNC 4672, Close-up of apex; **G** = Radula, SBMNH 169023, bar = 200 µm; **H** = *Neptunea alabaster*, RNC 4969, Pervenets Canyon, 913 m, 74.0 mm; RNC 4969, Radula, bar = 200 µm.





**Figure 2.** *Neptunea mcleani*. **A** = Holotype, LACM 3663, Bering Canyon, 1018 m. 106.8 mm; **B** = Close-up of sculpture (Paratype 2); **C** = Paratype 1, SBMNH 169022, Bering Canyon, 1065 m. 95.7 mm; **D** = Paratype 2, RNC 5050, S of Zhemchug, 818 m. 107.3 mm; **E** = RNC 5151, Bering Canyon, 414 m. 129.1 mm; **F** = Paratype 2, RNC 5050, Radula, bar = 200  $\mu$ m; **G** = SBMNH 169022/RNC 5052, egg capsules attached to skate egg case, Bering Canyon, 414 m. 15 x 10 mm; **H** = Close-up of egg capsules.



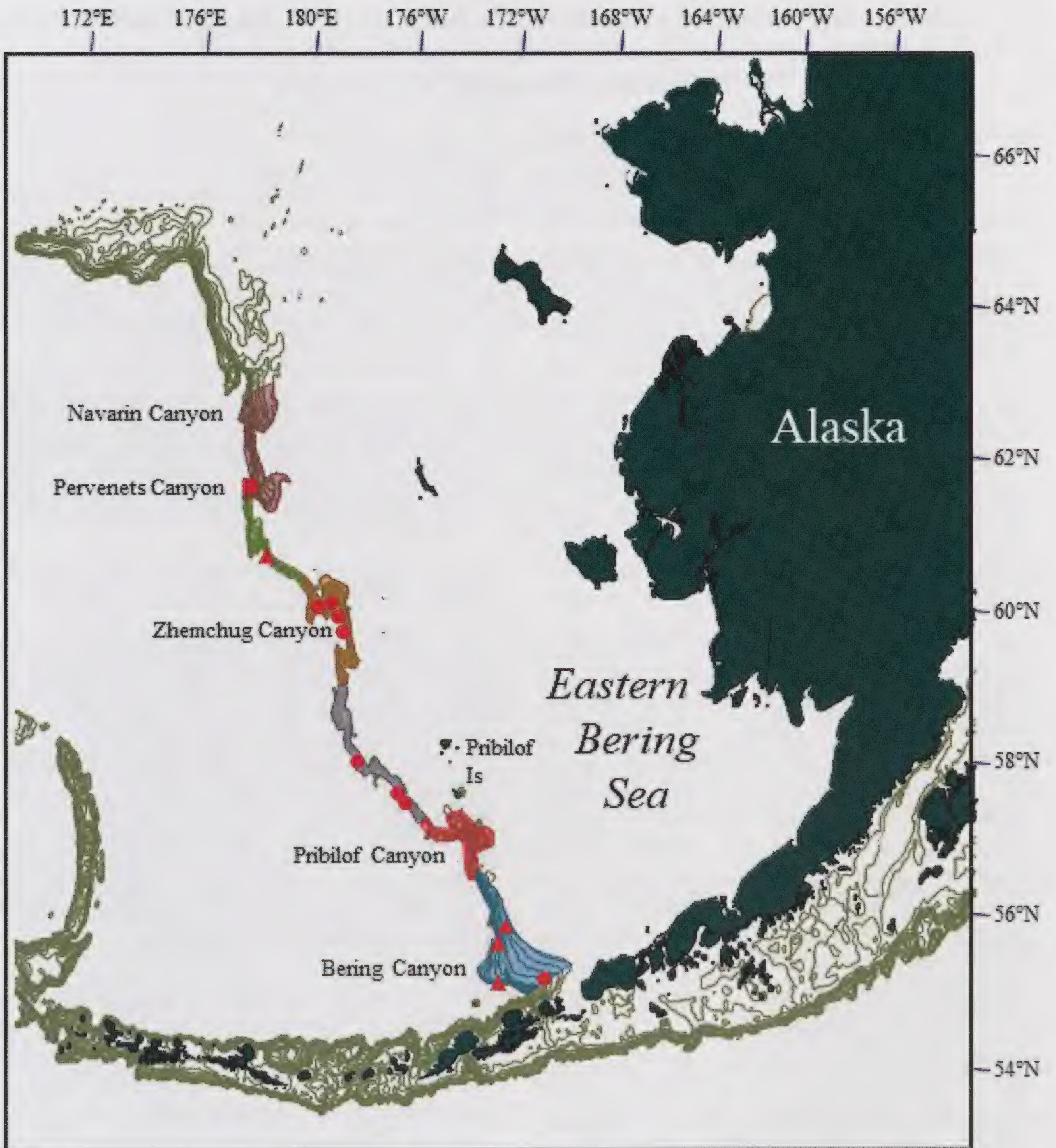


Figure 3. Distribution map Eastern Bering Sea.



## The Fossil Cypraeidae of the Fruitville Member (Unit 3) and Kissimmee River Valley Equivalent, Tamiami Formation of Southern Florida: (Mollusca: Gastropoda: Cypraeidae)

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**ABSTRACT** Four species of the *Pahayokea* (*Gardnericypraea*) Petuch and Drolshagen, 2011 subgenus are reclassified as *Akleistostoma* (*Gardnericypraea*) subgenus species. This represents a continuation of geographically separate, but parallel, evolutionary tracks throughout the Piacenzian Pliocene Tamiami Formation.

**KEYWORDS** Tamiami Formation, Fruitville Member (Unit 4), Black Layer, Unit 4 equivalent, Fruitville Member (Unit 3), Unit 3 equivalent, Unit 2 equivalent, Golden Gate Member, Cypraeidae, fossil, *Akleistostoma*, *Siphocypraea*, *Pahayokea*, *Calusacypraea*, *Okeechobea*, *Pseudadusta*, Myakka Lagoon System (Myakka), Sarasota area, Kissimmee Embayment, Kissimmee River Valley (Kissimmee), Polk Peninsula, Caloosahatchee Strait, Loxahatchee Strait

### INTRODUCTION

The transition from the highest sea levels of Unit 4 time to Unit 3 time at Myakka and Kissimmee was marked by falling sea levels as tropical conditions eased. This resulted in reduced and altered molluscan habitats and in the adaptive speciation of the Cypraeidae populations. The ten Fruitville Member (Unit 4) Cypraeidae species in five genera of the Myakka Lagoon System were followed by ten new species in four genera which evolved in Fruitville (Unit 3) time. In the Kissimmee River Valley, the nine Unit 4 equivalent species in three genera were reduced to four new species in two genera which emerged in that area. While *Okeechobea* (Petuch, 2004) Unit 3 equivalent species have not been recorded from Kissimmee, their presence may be inferred as species have been recorded from Unit 2 equivalent strata.

### Unit 3 Transition

The transition from the highest sea levels of the Tamiami subsea, which was the hallmark of Unit 4 time, to Unit 3 time at Myakka and Kissimmee was marked by falling sea levels, resulting in reduced and altered molluscan habitats. Tropical conditions still persisted, but were less intense. At this time, all Unit 4 Cypraeidae species were replaced by new species in a sequential evolution as the populations adapted to the altered habitats during the subsequent Unit 3 time.

Unit 3, along with Unit 4, also marked the highpoint of Cypraeidae diversity in the late Piacenzian Pliocene. The decline in diversity would not be precipitous, and included a significant interim reprieve during Unit 2 time. For the Cypraeidae genera this meant either adaptation or extinction.



### Fruitville (Unit 3) Myakka Lagoon System

In the western Myakka estuary and lagoon system, Fruitville Unit 3, present day Sarasota region, the receding sea levels reduced, but did not eliminate the mangrove forests, leaving significant remnants in the most seaward sections. However, the “Black Layer” which characterized Unit 4 was not dominant in Unit 3. The last of the *Akleistostoma* (*Paludacypraea*) Petuch and Drolshagen, 2011 species, *i.e.* *A. (P.) walleri* Petuch, Berschauer & Myers, 2018, was confined to this layer. Specimens exhibit the black/blue or tan staining associated with brackish, swamp like muddy estuaries. Other species inhabited the interspersed estuarine mud flats which also served as a shared habitat with the remnant Black Layer and intertidal shoals.

The adjacent seaward waters consisted of large quartz sand intertidal shoals which dominated the Cypraeidae habitats. These shoals hosted extensive beds of the pearly mussel *Perna conradiana* (d’Orbigny, 1852) which formed low, unlayered, massive reef like mounds, half buried in the substrate. Patches of sea grass were scattered between the mussel beds and hosted many of the Unit 3 Cypraeidae. These patches were associated with *Calusacypraea sarasotaensis* (Petuch, 1994) and *Calusacypraea (Myakkacpraea) kelleyi* (Petuch, 1998). They also hosted *Akleistostoma rilkoii* (Petuch, 1998), *Siphocypraea parodizi* (Petuch, 1994), *Pseudadusta kalafuti* (Petuch, 1994) and *Pseudadusta ketteri* (Petuch, 1994). These Unit 3 patches also hosted the first true *Siphocypraea* (Heilprin, 1886) species, *i.e.* *S. cannoni* Petuch, 1994.

Myakka Cypraeidae populations remained largely isolated in Unit 3 time. However, *P. ketteri* has been recorded in both Myakka and the Golden Gate of the Everglades Pseudoatoll in Lee and Collier Counties. However, the

neotenic Cypraeid genus *Calusacypraea* (Petuch, 1996) remained isolated in Myakka throughout Pinecrest and Fruitville times.

### Fruitville (Unit 3) Kissimmee River Valley Equivalent

In the east, despite the presence of extensive mangrove forests and mud flats within Kissimmee, the mangrove forests do not appear to have served as a principle Cypraeidae habitat during either Unit 4 or 3 equivalent time. While mud flats did serve as a habitat during Unit 4 equivalent time, by Unit 3 equivalent time, the remaining known Cypraeidae populations in the Rucks Pit and its southern extension habitats were living on sea grass beds and sand patches in the embayment. While no Index Fossils are available, the species were recorded from above Unit 4 equivalent facies. The sand patch facies at Rucks Pit were unchanged throughout both units. NOTE: Some Cypraeidae Unit 3 equivalent species and cf. species in the Dickerson Aggregates Pit habitats, approximately 2 km east of Rucks Pit, exhibit the black/blue and tan staining typical of mangrove habitats. As these were collected from spoil piles, a specific unit could not be assigned.

The receding sea levels had a dramatic effect upon the Cypraeidae populations in the Kissimmee Embayment and its southern sedimentary deposits. Only four species have been recorded from Unit 3 equivalent facies vs. eight from Unit 4 equivalent time. It is, however, noteworthy that while no *Okeechobea* Petuch, 2004 species have been recorded, their existence may be inferred as several species of the genus emerged during Unit 2 equivalent time.



### Unit 3 Ends

The end of Unit 3 time at Myakka was marked by the commencement of a second pulse of falling sea levels, albeit modest compared to the drop experienced from Unit 4 to Unit 3 time. This was caused by cooling temperatures. Sea

levels also dropped in Kissimmee. This resulted in altered habitats as reflected in Unit 2 and Unit 2 equivalent facies and species. This was an interim reprieve for the Cypraeidae populations and resulted in the last radiation and Cypraeidae speciation within the Piacenzian Pliocene Tamiami Formations.

### Fruitville Member Species – Unit 3 \*G = Also in the Golden Gate Member

Myakka Lagoon System (Sarasota)

*Akleistostoma rilko* (Petuch, 1998)

*Akleistostoma (Mansfieldicypraea) juliagardnerae* Petuch and Drolshagen, 2011

*Akleistostoma (Gardnericypraea) buchecki* (Petuch and Drolshagen, 2011)<sup>++</sup>

*Akleistostoma (Paludacypraea) walleri* Petuch, Berschauer & Myers, 2018

*Siphocypraea cannoni* Petuch, 1994

*Siphocypraea (Seminolecypraea) parodizi* Petuch, 1994

*Calusacypraea sarasotaensis* (Petuch, 1994)

*Calusacypraea (Myakkacypraea) kelleyi* (Petuch, 1998)

*Pseudadusta ketteri* (Petuch, 1994) \*G

*Pseudadusta (Bithloa) kalafuti* (Petuch, 1994)

Kissimmee Embayment (Kissimmee Valley restricted) Unit 3 equivalent

*Akleistostoma (Olssonicypraea) diegelae* (Petuch, 1994)

*Pahayokea penningtonorum* (Petuch, 1994)

*Pahayokea heimeri* Petuch and Drolshagen, 2011

*Pahayokea (Kissimmecypraea) leonardi* Petuch and Drolshagen, 2011

Table 1. Fruitville Member Species - Unit 3.

Altogether, 13 species in five genera have been collected in Fruitville Unit 3 deposits and its equivalent.

### RECLASSIFICATION<sup>++</sup>

In 1998, Petuch described three new species in Units 10, 7 and 4 from the Myakka Lagoon System (Sarasota area) which he classified in the subgenus *Siphocypraea* (*Akleistostoma*) Gardner, 1948 as follows:

Unit 10      *S. (A.) erici* (Petuch, 1998)

Unit 7      *S. (A.) mansfieldi* (Petuch, 1998)

Unit 4      *S. (A.) jenniferae* (Petuch, 1998)

In 2004, Petuch recognized *Akleistostoma* (Gardner, 1948) as a full genus, thereby reclassifying the three species above as *Akleistostoma* species. *Akleistostoma carolinensis* (Conrad, 1841) is the type species of the genus.

In 2004, the *Pahayokea* (Petuch, 2004) genus was also introduced as a subgenus of *Siphocypraea* Heilprin, 1886, representing an offshoot of the *Siphocypraea (Seminolecypraea) trippeana* Parodiz, 1998 lineage. *Pahayokea* species were described as broader, fatter shells



with well developed and often flaring margins as compared to *Siphocypraea* subspecies. The resemblance to *Akleistostoma* genus species in shell shape and general appearance was noted. However, the *Siphocypraea* features of a narrow aperture and a coiled apical sulcus, some more coiled than others, were determinative. *Pahayokea penningtonorum* Petuch, 1994 was designated as the type species. All species within the genus were restricted to the Kissimmee Embayment and River Valley.

In 2011, Petuch and Drolshagen recognized *Pahayokea* as a full genus and proposed the subgenus *Gardnericypraea* Petuch and Drolshagen, 2011 within the *Pahayokea* genus, placing all three *Akleistostoma* 2004 species and a newly described Unit 3 species within that subgenus. *Pahayokea (Gardnericypraea) mansfieldi* was designated the type species of the subgenus. At that time, the four species of the subgenus were classified as follows:

Unit 10	<i>P. (G.) erici</i> (Petuch, 1998)
Unit 7	<i>P. (G.) mansfieldi</i> (Petuch, 1998)
Unit 4	<i>P. (G.) jenniferae</i> (Petuch, 1998)
Unit 3	<i>P. (G.) buchecki</i> Petuch and Drolshagen, 2011

The subgenus represented large, highly inflated cowries that lack recurved apical sulci (*i.e.* a coiled apical sulcus) and have wide, flaring apertures. This does not accord with *Pahayokea* genus described features, *i.e.* coiled apical sulci and narrow apertures. In comparison, all *Akleistostoma* species show a wide range of features, but all also share an essentially straight or slightly recurved apical sulci and wide, open and widening apertures. The contradictions with true *Pahayokea* species do not support the status of the *Gardnericypraea* as a subgenus of *Pahayokea*.

The four species were also considered the root stock for the *Pahayokea* genus, although all four species were restricted to the Myakka Lagoon System. However, Kissimmee is separated and isolated from Myakka by the massive Polk Peninsula to the west as well as the narrow, deep water Caloosahatchee and Loxahatchee Straits to the south. In addition, intracapsular direct development and the associated restricted migration may be inferred based on the sister genus, *Muracypraea* Woodring, 1957 and the Recent *Muracypraea mus* Linnaeus, 1758 complex. The absence of a viable path of migration into Kissimmee from Myakka means the status of the subgenus species as the root stock for the *Pahayokea* genus, restricted to Kissimmee, is unsupported.

In summary, the features of the four species of the subgenera do support their reclassification as *Akleistostoma (Gardnericypraea)* species and they are reclassified as follows:

Unit 10	<i>Akleistostoma (Gardnericypraea) erici</i> (Petuch, 1998)
Unit 7	<i>Akleistostoma (Gardnericypraea) mansfieldi</i> (Petuch, 1998)
Unit 4	<i>Akleistostoma (Gardnericypraea) jenniferae</i> (Petuch, 1998)
Unit 3	<i>Akleistostoma (Gardnericypraea) buchecki</i> (Petuch and Drolshagen, 2011)

See Figure 3 for comparisons with *Pahayokea penningtonorum*, type species of the genus.

True *Pahayokea* species of the Piacenzian Pliocene, Tamiami Formation were confined to Kissimmee until the end of the Pliocene (Fruitville Unit 2 equivalent). The Early, Middle and Latest Gelasian Age, Early Pleistocene, saw low sea levels throughout southern Florida, facilitating the migration and emergence of *Pahayokea* species to the south and west



southwest of Kissimmee in the Caloosahatchee Formation. The genus did not survive past the Latest Gelasian Age.

## Origins

At Sarasota, *A. rilko* resembles the older *Akleistostoma olssoni* Petuch and Drolshagen, 2011, but is stubbier and more rectangular while *A. (M.) juliagardnerae* and *A. (G.) buchecki* are most similar to the older *A. (G.) jenniferae* (Petuch, 1998). The former is a more rounded shell with less developed auricular flanges while the latter is a larger, more elongate shell. The *A. (P.) walleri* specimens share features of both Unit 4 *Paludacypraea* Petuch and Drolshagen, 2011, i.e. *cookei* and *fruitvillensis* Petuch and Drolshagen, 2011, but are larger, more elongate shells, with wider, more flaring apertures. Both *A. (S.) parodizi* and *S. cannoni* inhabited the sea grass beds associated with the pearly mussel beds (*Perna contradiana*). The former resembles the older *Siphocypraea (Seminolecypraea) grovesi* Petuch, 2004 while the latter is probably an offshoot of the *Seminolecypraea* Petuch and Drolshagen, 2011 subgenus, precursors of true *Siphocypraea* Heilprin, 1886. The origin of *C. sarasotaensis* is uncertain, but resembles the younger *Calusacypraea loxa* Petuch and Drolshagen, 2011. In contrast, *C. (M.) kelleyi* resembles the older *Calusacypraea (Myakkacypraea) myakka* Petuch, 2004 but is more fusiform (spindle-like) and has a much narrower aperture. Found in both the Sarasota and Golden Gate quarries, *P. ketteri* is most similar to the older *Pseudadusta metae* (Petuch, 1994) while *P. (B.) kalafuti* resembles the older *Pseudadusta (Bithloa) irisae* Petuch and Drolshagen, 2011.

At Kissimmee, *A. (O.) diegelae* resembles an extreme dwarf of the older *Akleistostoma (Olssonicypraea) bairdi* (Petuch, 1994). *Pahayokea penningtonorum*, type of the genus,

is most similar to the older *Pahayokea gabriellae* (Petuch, 2004) but is smaller, narrower and higher domed. Similar to *Pahayokea basingerensis* (Petuch, 2004), *P. heimeri* is more oval and stumpier than the former. *Pahayokea (Kissimmecypraea) leonardi* comes in two forms. The original description was based on the smaller form which, compared to *Pahayokea (Kissimmecypraea) eddiematchetti* Petuch and Drolshagen, 2011, is average in size but is smaller than *P. (K.) eddiematchetti*, more oval, inflated with a more rounded base, narrower aperture and smaller and more pointed auricles. The larger form shares these features, but is larger and more elongate.

## ACKNOWLEDGEMENTS

This article is based in large part on the related collective works of Dr. Edward J. Petuch which encapsulate his 45 years of field and academic work with the geology, paleogeography and fossil fauna of Florida.

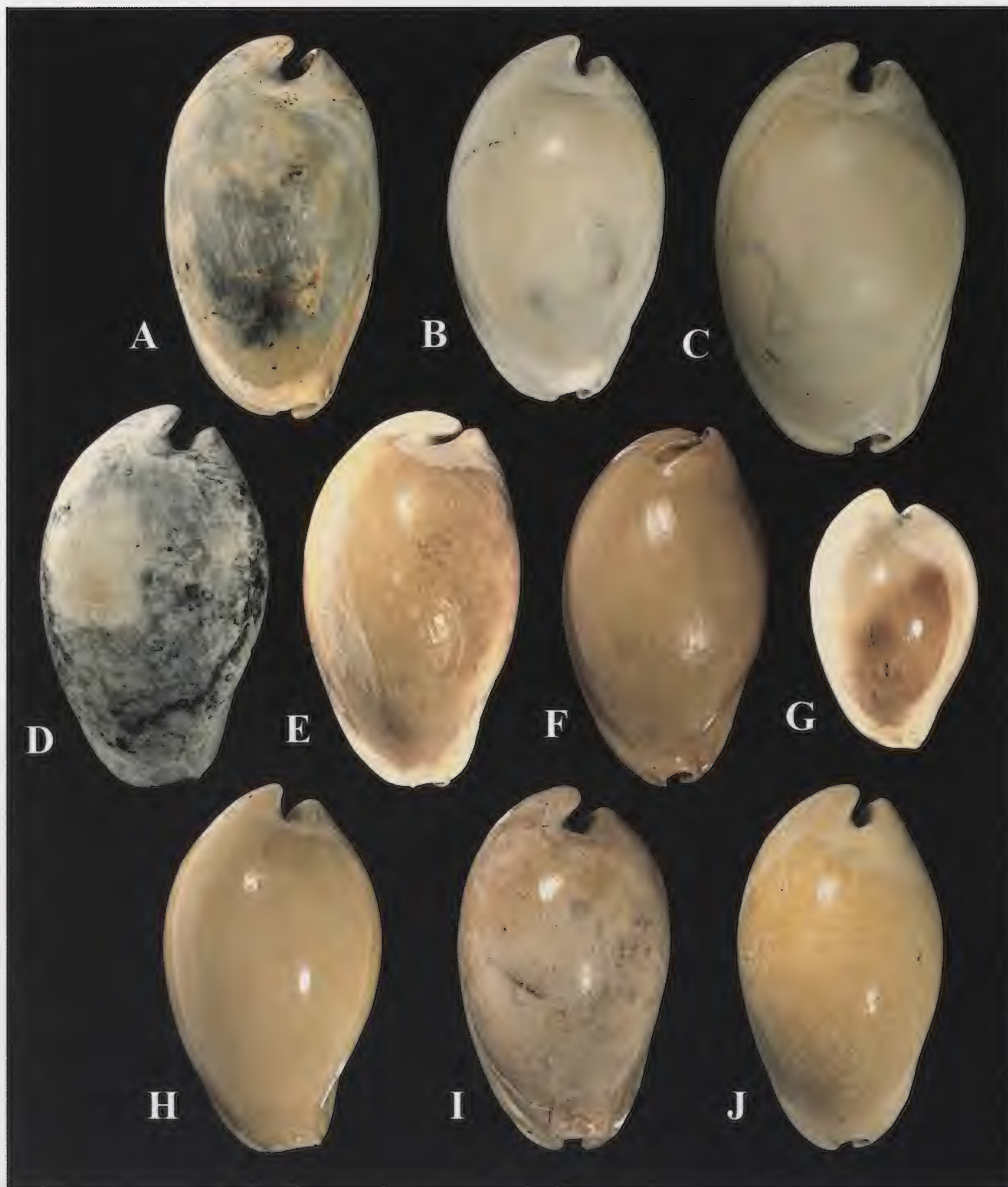
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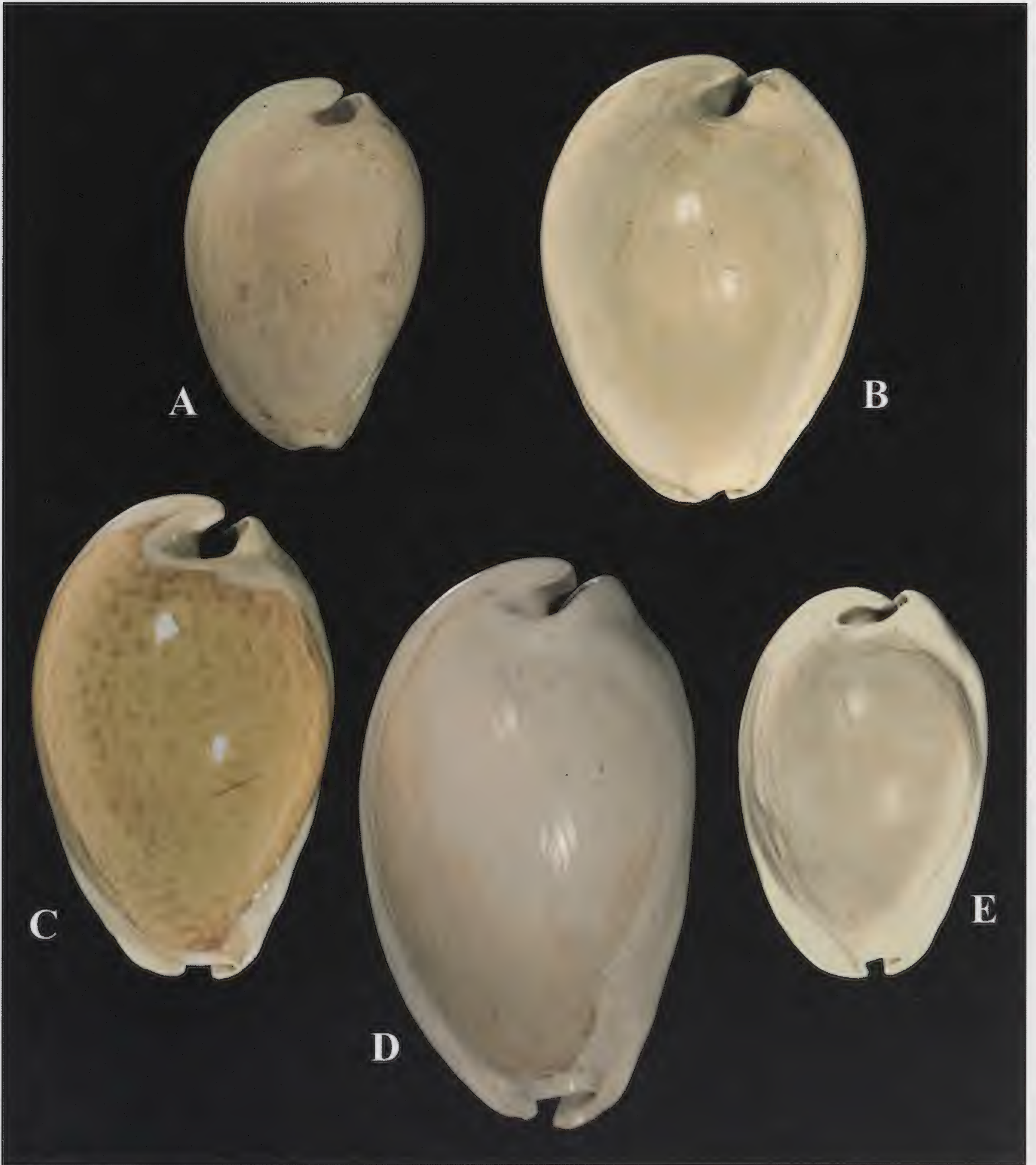
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**Figure 1. Myakka Lagoon System, Sarasota (Unit 3).** A = *Akleistostoma rilko*i (Petuch, 1998), length = 66.8 mm; B = *Akleistostoma* (*Mansfieldicypraea*) *juliagardnerae* Petuch and Drolshagen, 2011, length = 64.0 mm; C = *Akleistostoma* (*Gardnericypraea*) *buckecki* Petuch and Drolshagen, 2011, 79.4 mm; D = *Akleistostoma* (*Paludacypraea*) *walleri* Petuch and Drolshagen, 2011, length = 72.8 mm; E = *Siphocypraea cannoni* (Petuch, 1994), length = 74.5 mm; F = *Siphocypraea* (*Seminolecypraea*) *parodizi* Petuch, 1994, length = 67.9 mm; G = *Calusacypraea sarasotaensis* (Petuch, 1994), length = 44.4 mm; H = *Calusacypraea* (*Myakkacypraea*) *kelleyi* (Petuch, 1998), length = 58.4 mm; I = *Pseudadusta ketteri* (Petuch, 1994), length 54.3 mm; J = *Pseudadusta* (*Bithloa*) *kalafuti* (Petuch, 1994), length = 74.1 mm.





**Figure 2. Kissimmee River Valley restricted (Unit 3 equivalent).** A = *Akleistostoma (Olssonicypraea) diegelae* (Petuch, 1994, length = 42.8 mm; B = *Pahayokea heimeri* (Petuch and Drolshagen, 2011), length = 51.6 mm; C = *Pahayokea (Kissimmecypraea) leonardi* Petuch and Drolshagen, 2011, length = 58.5 mm; D = *Pahayokea (Kissimmecypraea) leonardi* Petuch and Drolshagen, length = 71.3 mm LARGE FORM; E = *Pahayokea penningtonorum* (Petuch, 1994), length = 49.8 mm.





Figure 3. Subgenus (*Gardnericypraea*), *Akleistostoma* vs. *Pahayokea* Comparisons. A = *Pahayokea penningtonorum*, length = 47.7 mm (**Type of the genus**); B = *Akleistostoma carolinensis*, length = 60.3 mm (**Type of the genus**); C = *Akleistostoma* (*Gardnericypraea*) *erici* (Petuch, 1998), length = 75.9 mm; D = *Akleistostoma* (*Gardnericypraea*) *mansfieldi* (Petuch, 1998), length = 67.3 mm; E = *Akleistostoma* (*Gardnericypraea*) *jenniferae* (Petuch, 1998), length = 63.6 mm; F = *Akleistostoma* (*Gardnericypraea*) *buckhecki* Petuch and Drolshagen, 2011, length = 79.4 mm.



## Corrections to the Gender Assignment of Recently Named Species of *Asperitas* and *Papuina*

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**ABSTRACT** The following are corrections to the gender assignment of recently published names of two snails from Indonesia. The names as originally published by Parsons (2019a, b) are *Asperitas bimaensis abbasianus* Parsons, 2019 from western Sumbawa and *Papuina abbasianus* Parsons, 2019 from Nabire, Papua. The corrected names are *Asperitas bimaensis abbasiana* and *Papuina abbasiana*.

**KEY WORDS** *Asperitas bimaensis abbasiana*, *Papuina abbasiana*

### DISCUSSION

The recently established names of *Asperitas bimaensis abbasianus* Parsons, 2019 and *Papuina abbasianus* Parsons, 2019, both have incorrect gender assignments applied to the subspecies and species names by original description.

The gender for both *Asperitas* and *Papuina* is feminine. Therefore, I hereby correct the names to read as *Asperitas bimaensis abbasiana* and *Papuina abbasiana* respectively, for the whole of their respective papers. The gender assignment correction has been made on the Internet at the MolluscaBase website for the Papuan snail, *Papuina abbasiana* (Bouchet, 2019b), but as of yet it has not been made for the Sumbawan snail, *Asperitas bimaensis abbasianus* (Bouchet, 2019a).

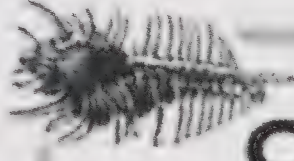
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## Spelling Correction of a Sumatran Subspecies of *Amphidromus* Albers, 1850

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**ABSTRACT** The following are spelling corrections to the names of two rare arboreal snails from Sumatra. The names as originally published by Parsons and Abbas (2016) are *Amphidromus* (*Goniodromus*) *bulowi* Fruhstorfer, 1905 from Mount Singgalang, West Sumatra; and *Amphidromus* (*Goniodromus*) *bulowi malalakensis* Parsons and Abbas, 2016 from Bukit Pandan western Malalak District, West Sumatra. The corrected names are *Amphidromus* (*Goniodromus*) *buelowi* and *Amphidromus* (*Goniodromus*) *buelowi malalakensis*.

**KEY WORDS** *Amphidromus* (*Goniodromus*) *buelowi*, *Amphidromus* (*Goniodromus*) *buelowi malalakensis*

### DISCUSSION

Since publishing the paper establishing the new subspecies *Amphidromus* (*Goniodromus*) *bulowi malalakensis* Parsons and Abbas, 2016, it has come to light that a quoted rule from the current zoological nomenclatural code (ICZN, 1999) was not read in its entirety, namely Article 32.5.2. According to the second part of this ICZN article, 32.5.2.1, if a species name bearing a diacritic is published before 1985 and based on a German word, such as the surname Bülow, then the umlaut is removed from above the vowel and “e” is placed after it.

Based on this rule, the original spelling of *A. (G.) bulowi* Fruhstorfer, 1905 actually should have been corrected to *A. (G.) buelowi*. This means that the recently named subspecies should have its spelling corrected to *A. (G.) buelowi malalakensis*. This correction has been made on the Internet at MolluscaBase website (Bouchet, 2016). The spelling corrections apply to usage of both names throughout the paper, except

under parts of the “Taxonomic and other remarks” in the Materials and Methods section.

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## CLUB NEWS

### 2019 November General Meeting and Fall Auction

Our November general meeting, elections, and fall auction were held on Saturday November 16, 2019, at David and Felicia Berschauer's home in Laguna Hills. We had an incredible turn out with members from four counties (and out of State) present. The auction was a great success. The income from this auction was the second highest ever recorded. Many of these shells were from the Pratt Collection. Thanks to all those who helped in selecting shells, cleaning shells, labeling shells, bagging shells, setting up the silent and verbal auction tables, printing up and assigning the silent auction bid sheets and preparing the auction list for the event. Special thanks to our honorable auctioneer, David Berschauer, to those who attended and those who purchased shells. The big sale items were the *Lycinia leucodon*, *Austrotrophon catalinensis*, *Zoila jeaniana sherylae* and *Cymbiola palawanica*.

### 2019 Holiday Party

This year's Holiday party was especially nice. It was held at Jill and Todd Spofford's home in San Diego on December 14, 2019, with spectacular Italian cuisine. We had a good turn out with members from three counties present. Highlights of the party included a beautiful venue, great catered Italian food (with Spumoni for desert), fantastic friends, some shells, our secret gift exchange, raffle prizes.

### 2020 January General Meeting

Our January general meeting held at 7:00 p.m. on January 16, 2020, in Room 104 at Balboa Park in San Diego. Four Club members gave short talks about their favorite shell. After the presentations members showed off their shells and had general discussions.





## President's Message

Roger N. Clark  
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Happy 2020! I am pleased and honored to be elected your President for the 2020 calendar year, and would like to thank you for your support. I would also like to congratulate the other elected members of the 2020 Board of Directors, Bill Schramm, Lisa Dawn Lindahl, Leo Kempczenski, John "Duffy" Daughenbaugh and David Michaelski. This is going to be an exciting year for the San Diego Shell Club. With the new year, we hope to expand membership in the Club and welcome back many former members!

As we start this New Year, I will be focusing my efforts in several key areas: membership, technology, field trips, and attendance. First and foremost will be increasing membership, which at the end of 2019, was about 200 members worldwide. My continued efforts in this regard will require reaching out to shell collectors and promoting our Club throughout the United States and overseas. We have developed a world class journal that has one of the largest distributions. Let's keep those marvelous articles coming for The Festivus.

We plan on using technology to make it easier for our members, and people who may be interested in becoming members, to enjoy our meetings, scheduled talks, and auctions. Last fall we did a live streaming of our Fall Auction on Facebook so that people could watch our auction in real time. We intend to have live broadcasts of future presentations, auctions, and perhaps other events during the 2020 calendar year. We also hope to organize some Club collecting trips, perhaps to Baja California or the Sea of Cortez, and possibly some diving or dredging trips.

Once again, we have secured the large exhibit room this year for the 5<sup>th</sup> annual West Coast Shell Show, which allows us to provide more space for exhibitors, dealers, and world class presentations in the field of Conchology. With Lisa Dawn Lindahl's efforts we will also be promoting more shell arts by local artists, who will have the opportunity to exhibit, compete and sell. We hope to expand participation in the competitive exhibit categories and will be extending invitations to members of other shell clubs to participate in the West Coast Shell Show this year from 21<sup>st</sup> to 23<sup>rd</sup> August, 2020. Lets make 2020 the best year to date for the San Diego Shell Club!



## Editor's Corner - How we got here

David P. Berschauer, Editor  
[shellcollection@hotmail.com](mailto:shellcollection@hotmail.com)

Our journal is now in its 52<sup>nd</sup> volume, and it seems hard to believe that it has been six years since we began the new format of The Festivus. Reflecting back on where we have been and how we got here is important. This journal began as a humble news letter for our Club back in 1970, edited by Blanche Brewer. Shortly thereafter in 1976 Carole Hertz became the editor and made changes to the format and content of the newsletter. Under Carole's vision The Festivus became more scientific and less of a "clubby" newsletter. Ultimately under Carole's leadership, and with a lot of hard work and dedication, what began as a monthly club newsletter morphed into a scientific peer reviewed journal. For decades the journal was typed on an old fashioned typewriter, and printed in black and white on copy paper. Ultimately, with the advent of computers and word processing, the journal began looking more professional, however it remained black and white - with the occasional color page inserted. Carole Hertz devoted 37 years of passion, vision, and hard work into editing and publishing The Festivus - eleven months a year. After doing such an amazing job for so long Carole retired as editor in 2014.

The Club's Board of Directors made a committee to find a new editor. David Waller and I were the only members of that committee. It seemed that no one wanted the job as editor because Carole set the proverbial bar so high that no one felt that they could fill her shoes. Just like the kid's game of "hot potato" we were "it". What to do, and developing a vision for the future were tough questions. We looked at the other journals then in print, and I sought out advice from professionals. First, we decided to make the journal available as an electronic copy (PDF format) on a quarterly basis, in keeping with the modern trend. The concern here was that no one would want to pay for printed copies and that the printed format might die. Second, we realized that the old black and white format had to go, and that we needed to print in color and in magazine format. I remembered that Tom Rice's publication, *Of Sea and Shore*, had such beautiful and professional covers in the last years of publication, and that became the model for our new look. Third, we studied the organization and layout of professional publications and the better club magazines and came up with what we felt was a good plan and design. I spoke with my old friend and mentor James McLean, the Curator of Malacology at the Los Angeles County Museum of Natural History. James' advice was invaluable, among many other things he said "if you want to get good articles you have to publish new taxa." Daniel Geiger (of the Santa Barbara Museum of Natural History) spent hours with me on the phone, mentoring and giving advice on how to organize and lay out the journal, how to solicit and work with peer reviewers, and how to edit the journal. Many other professionals were kind enough to provide advice, suggestions and feedback. Ultimately we went with their advice and made the former "peer review board" an open (and ever expanding) group of confidential peer reviewers; this enabled us to seek review from dozens of experts in different specialties as needed, and not overburden a few experts with several papers each issue. Our current beautiful covers are designed and produced by Rex Stilwill, a professional graphics designer, and often feature images of live mollusks.

Today our journal, The Festivus, is electronically published to over 200 people and institutions worldwide, and about 80% of our members also receive paper copies; we are also reprinted (after two years) on the Biodiversity Heritage Library to provide wider coverage. Advertising helps defray costs of publishing and keeps member's costs affordable.



### Book review of: “Cone Shells of the Seychelles”

by David Touitou, 2019, 174 pages, 36 color plates, and 32 color images of individual live animals. ISBN 978-2-9566508-0-12. Available in English or French from Conchbooks, MdM Shell Books, Naturama and eBay. Cost is approximately \$46 US.

Paul M. Tuskes

Mr. Tourtou does excellent photography, which is reflected in the quality of both the colored plates and under-water life history photographs. The book only addresses identification of Seychelles cones. The author has reviewed past publications, visited various museums, and lived in the Seychelles. He provides lists, text, and photos of cones positively known from the Seychelles, those that may occur there, and those, which he believes are incorrectly cited from those islands.

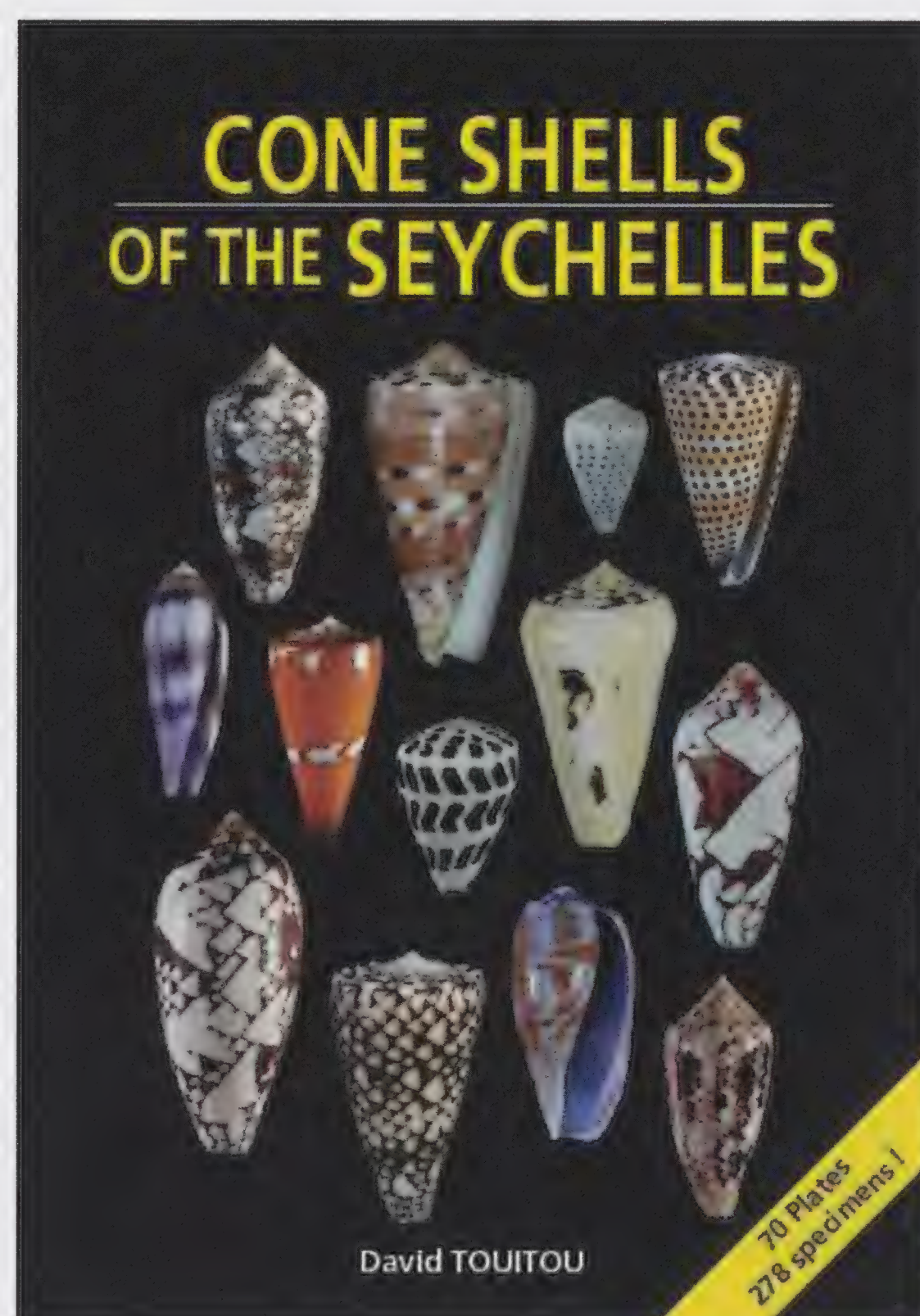
A number of taxonomic schemes for the Conidae have been previously published. To address future adjustments to Cone systematics, both the text and plates are arranged in alphabetical order, rather than organized by genus.

The species format is consistent from one species to the next making it easy to find the information you are looking for: size, habitat, depth, distribution, and additional notes are provided for each species. Typically, multiple specimens of each species are illustrated to document expected variation. Various features of shell morphology and coloration are illustrated to assist with terminology used in the text.

A more detailed map of the Seychelles would have been appreciated. The introductory text is written in a casual chatty manner with a few structural issues, which may have resulted in the translation from French to English. The small format book, approximately 15 x 21 cm makes it easy to take the book on trips. The binding is stiff so the book promptly closes and will not lay flat.

The text does not address biogeography of this group, or the contribution made to the fauna of the Seychelles by surrounding area. The harpoon-like radulas of cones with various dietary needs are well illustrated but there is no informative discussion of cone toxins, and the bibliography is surprisingly sparse. These additions would have expanded the value of the book beyond cone identification and delivered relevant information to the reader.

This book represents the next step in our knowledge of the cones occurring in the Seychelles. As more islands in the archipelagos are surveyed, more surprises will appear. The book is focused on cone identification of the Seychelles and does a good job of it.





## *Zoila jeaniana jeaniana* vs. *jeaniana sherylae*

David B. Waller  
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I created this column to help collectors identify and distinguish different species of Cypraeidae, one of the most commonly collected families of marine gastropods. This is a relatively large family of mollusks and there are often unique morphologies that clearly identify one species from another. Other information such as location data can also be helpful in making an accurate identification. Since I am not an expert, but more of an enthusiast, I will be researching particular species that are similar in appearance to expose those unique morphologies and present them here with the hopes that my readers will submit their observations and/or modifications for publication in preceding issues. For this column, I review some of the information from popular publications that distinguish *Zoila jeaniana jeaniana* (Cate, 1968) from *Z. jeaniana jeaniana sherylae* (Raybaudi, 1990), two species that look very similar but whose values can differ by several hundred dollars. Worldwide Mollusc Species Data Base ([www.bagniliggia.it](http://www.bagniliggia.it)) and MolluscaBase ([www.molluscabase.org](http://www.molluscabase.org)) list four *Zoila jeaniana* subspecies: “*jeaniana* (Cate, 1968); *aurata* Raybaudi, 1979; *sherylae* Raybaudi, 1979; and *thalamega* Lorenz, 2002”. *Zoila j. aurata* and *j. thalamega* are primarily distinguishable from *j. jeaniana* and *j. sherylae* by color and shape respectively; the base color of *j. aurata* is generally white-cream with light orange brown-orange dorsal and terminal markings, in some cases, the base may also be light orange-orange, while *j. thalamega* has a shape more recognizable with *Z. friendii friendii*. Differentiating *j. jeaniana* from *j. sherylae* is more difficult because these subspecies have similar size, shape, color and dorsal markings.

### DIAGNOSIS

*Z. jeaniana jeaniana*, (C.N. Cate, The Veliger, Vol. 10(3):222-224, 1968, Holotype: 76 mm trawled off Bernier Island, Dirk Hartog Shelf at 75 m, Western Australian Museum (Perth), Reg. No. C3465). “Shell large, strong, lightweight, humped, globular-ovate; base sloping inward from the outer margin; lip base flat, columellar base perceptibly convex; terminals prominent, thin-sided, sharply edged, and more thickly and roundly formed in front; margins acutely angled, only thinly calloused, vertically broad, with granular texture; aperture straight, curving abruptly left adapically; teeth numerous, medium in length, strong, well defined, particularly on abaxial margin of fossula; fossula deep, without denticles, milk-white in color; primary shell color on dorsum light grey, with approximately three narrow white transverse bands, all of which can be seen through an irregular outer layer of light chestnut-brown, which becomes an irregular, darker color immediately above the lateral margin; broad margins are off-white, with faint touches of beige, loosely marked otherwise with large dark brown spots; base dark chestnut-brown, with same coloring extending over half the length of each interstices; other half of teeth and interstices off-white.”



Monograph of the Living Zoila, 2001, F. Lorenz: “Elongate-oval and heavy, dorsum slightly humped, base distinctly flattened, margins rather angular. Dentition on columellar side often distinct. Sharp extremities. Variable coloration from white to very dark dorsally, margins spotted with dark. Base varies from dark brown to black.” Location was reported as “Montebello Islands to Abrolhos Island Western Australia” found at depths of 35 to 150 m with a size range of “30 to 101 mm.”

Australia’s Spectacular Cowries, 2004, B. Wilson and P. Clarkson: “Shells tumid to lenticular, tending to be flat-based; anterior and posterior canals not up-turned or sharp edged. Aperture dentition fine, usually along whole length of columella; anterior teeth moderately strong as in the nominate subspecies but those at centre and anterior end of the columellar lip comprising short, vestigial denticles. Colour pattern as in the nominate subspecies except that sides generally lack a heavy overlay of chocolate so that the lateral spots are predominant on a mottled, creamy-grey to greenish-grey background, thus emphasizing terminal blotches, base chocolate brown, cream-gold or orange. Deep-water specimens (*i.e.*, from below 100 m) white or cream, basal and lateral pigmentation, if present, reduced to shades of tan or golden orange; lateral and dorsal spots, if present, pale tan.”

Cowries, A Guide to the Gastropod Family Cypraeidae, 2017, F. Lorenz: “Elongate-oval, heavy and inflated. Dentition on columellar side often indistinct. Sharp extremities.” Location is reported as “Coral Bay to Abrolhos Island, Western Australia” with a size range of “38 to 99 mm.”

*Z. jeaniana sherylae*, (L. Raybaudi, La Conchiglia, Vol. 253 255, pages 24-27, 1990). “This *jeaniana sherylae* is sensibly different from *jeaniana jeaniana*. Its size is normally much smaller. The columellar teeth are often less regular and complete. The basis is always black - at least in the specimens I have had - or almost black; on the contrary the basis color of *jeaniana jeaniana* ranges from white ivory to light brown, or coffee colour or orange or very light brown. The outline itself is sensibly different and the tips are slightly different.”

Monograph of the Living Zoila, 2001, F. Lorenz: “Smaller, with dark tips. Base black. Columellar teeth often less distinct” found in the “Point Quobba area, Western Australia.” The size range of “56-74 mm” is noted on plate 35.

Australia’s Spectacular Cowries, 2004, B. Wilson and P. Clarkson: “The shells tend to have the same flat base as topotypes but are relatively small (commonly on the 60-70 mm range) and have greyish tint on the sides. As noted earlier, columellar dentition is relatively weak in specimens from this population, with about 40% of shells actually lacking countable denticles posteriorly.”

Cowries, A Guide to the Gastropod Family Cypraeidae, 2017, F. Lorenz “Depressed. Base less calloused, dark brown to black. Margins rounded. Dorsum blue, with brown spotting.” Size range from “26 to 88 mm.” This description further raises *j. sherylae* from a forma to a subspecies based on mDNA analysis.



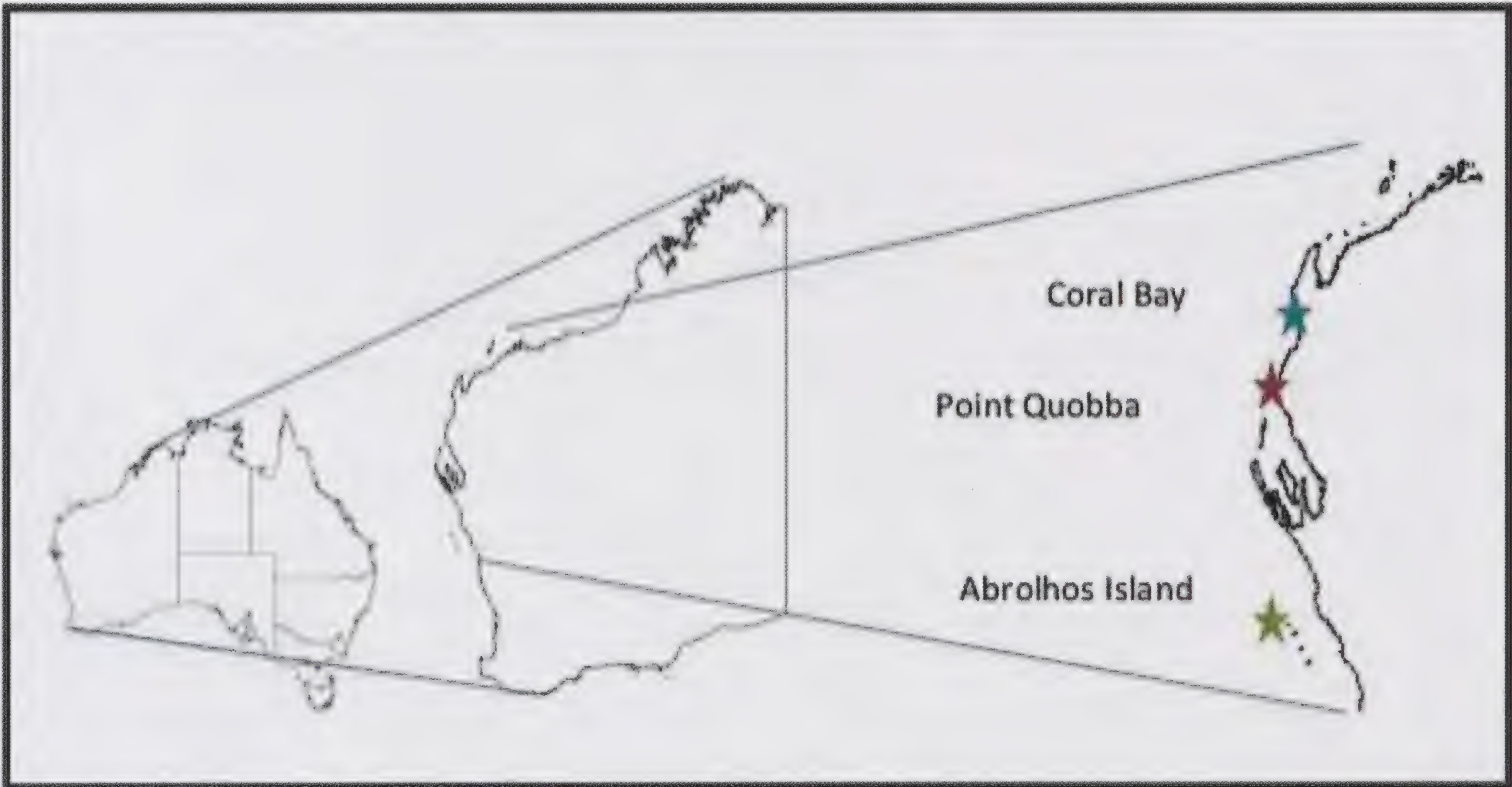


Figure 1. Locations of area range where *Z. jeaniana* are found.

Subspecies	<i>Z. j. jeaniana</i>	<i>Z. j. sherylae</i>	Comments
Described	C.N. Cate The Veliger, 10(3):222-224, 1968.	L. Raybaudi, La Conchiglia, 253 255: 24-27, 1990.	Publication date reported by MolluscaBase for <i>j. sherylae</i> should be 1990.
Size	38 mm to 99 mm	26 mm to 88 mm	<i>j. sherylae</i> size range falls within that for <i>j. jeaniana</i> .
Weight	Heavy, solid.	Less heavy, less solid.	Subjective
Dorsum Coloration	White, to very dark and mottled.	Blue with brown spotting.	<i>j. jeaniana</i> does not usually have a blue base coloration on the dorsum.
Base Coloration	White, all shades of orange, greenish brown to black.	Dark brown to black.	<i>j. sherylae</i> base color falls within that for <i>j. jeaniana</i> .
Margin Coloration	Dark spotting, with creamy-grey to greenish-grey band (“halo”) separating the margins from the dorsum.	Dark spotting, no “halo” separation reported between dorsal pattern and margins. Greyish tint on the sides.	<i>j. sherylae</i> does not usually have a halo separation.
Teeth	Dentition on columellar side rather indistinct.	Columellar teeth often less distinct.	Dentition for both subspecies varies substantially.
Location	Coral Bay to Abrolhos Island, Western Australia.	Point Quobba, Western Australia.	<i>j. sherylae</i> location falls within that for <i>j. jeaniana</i> .

Table 1. Comparison of information on *Z. j. jeaniana* and *Z. j. sherylae* from diagnoses above.



Characteristics distinguishing *Z. j. jeaniana* from *Z. j. sherylae* that may be helpful are shown in red (Table 2). Plates 1-6 show 12 specimens (6 *Z. j. jeaniana* and 6 *Z. j. sherylae*) for reference showing these characteristics.

Subspecies	<i>Z. j. jeaniana</i>	<i>Z. j. sherylae</i>
<b>Dorsum Coloration</b>	White to cream color with brown to black mottled markings.	Blue embryonic banding covered with brown spotting.
<b>Base Coloration</b>	Variable may be uniform dark brown to black or may have shades of light brown to black.	Uniform dark brown to black.
<b>Margin Coloration</b>	White to cream with dark brown to black spotting, often having a blue or white band (“halo”) separating the margins from the dorsum.	Grey brown to cream with dark brown or black spotting, no “halo” separation between dorsal pattern and margins.
<b>Location</b>	Coral Bay to Abrolhos Island, Western Australia.	Point Quobba, Western Australia.

**Table 2.** Distinguishing characteristics *Z. j. jeaniana* and *Z. j. sherylae* from specimens shown in plates 1-6.

Plate 7 compares *j. jeaniana* and *j. sherylae* showing the blue (embryonic banding) on the dorsum, just under the dark spotting on *j. sherylae*, characteristic of this species. However, the blue banding may be covered by the dark dorsal spotting as seen in image F. Correspondingly, the embryonic banding of *j. jeaniana* can be seen in some specimens as shown in image E.

Plate 8 compares the base coloration of *j. jeaniana* and *j. sherylae* showing the variable base color of *j. jeaniana* as seen in images A-C and the consistent dark base of *j. sherylae* as seen in images D-F. However, *j. jeaniana* can have a dark base characteristic of *j. sherylae* as seen in image C, while lesser developed specimens of *j. sherylae* may have lighter colored bases as seen in image G.

Plate 9 compares the marginal coloration of *j. jeaniana* and *j. sherylae* showing the characteristic blue and/or white margin separation between the dorsum pattern and perimeter spotting of *j. jeaniana* seen in images A-B. *Z. j. sherylae* is not characterized as having this unique coloration as seen in images C-D. However, not all *j. jeaniana* exhibit this characteristic as seen in image E and some *j. sherylae* appear to express a similar type separation as seen in image F.

It appears that, while the presence of one or more of these unique characteristics may be diagnostic for these species, having all of them in conjunction with appropriate location data may confirm the identity of your specimen. I welcome your comments and thoughts regarding other characteristics that you may be aware of to help others identify these species.

**Plates 1-6.** Plate 1 = dorsum views, Plate 2 = base views, Plate 3 = right side views, Plate 4 = left side views, Plate 5 = posterior end views and, Plate 6 = anterior end views, of *j. jeaniana* in rows one and two with *j. sherylae* in rows three and four. From right to left: (*j. jeaniana*) **A** = 75.8 mm, Western Australia trawled at 60-100 M (ex L. Buck Collection); **B** = 63.0 mm, Northwest Australia, trawled at 300 M; **C** = 67.7 mm, Exmouth Gulf, Western Australia diver taken at 60 M (ex M. Cooper Collection); **D** = 74.3 mm, north of Shark Bay diver taken at 45 M; **E** = 71.9 mm, north of Carnarvon, diver taken at 35 M (ex L. Buck Collection); **F** = 66.1 mm, Gnarlaloo diver taken at 45 M, (*j. sherylae*) **G** = 71.7 mm, Point Quobba diver taken at 30 M (ex J. Jackson Collection); **H** = 62.3 mm, Point Quobba diver taken at 20-30 M; **I** = 57.6 mm, Point Quobba diver taken at 28-32 M; **J** = 77.9 mm, Point Quobba diver taken at 26 M (ex J. Jackson Collection); **K** = 67.0 mm, Point Quobba diver taken at 35 M; and **L** = 71.7 mm, Point Quobba diver taken at 10 M (ex D. McBride Collection).





Plate 1. Dorsal views.





Plate 2. Base views.



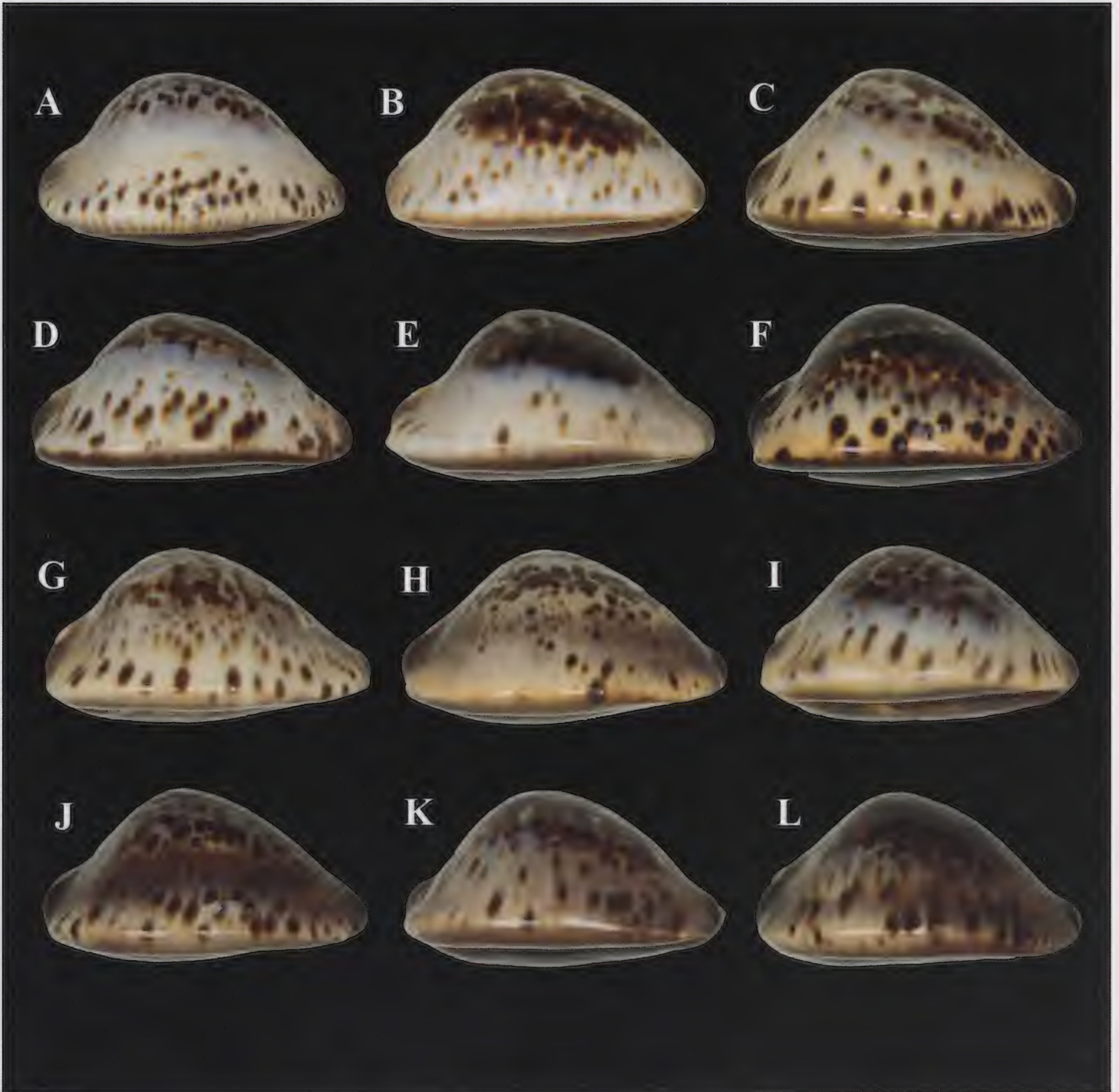


Plate 3. Right side views.



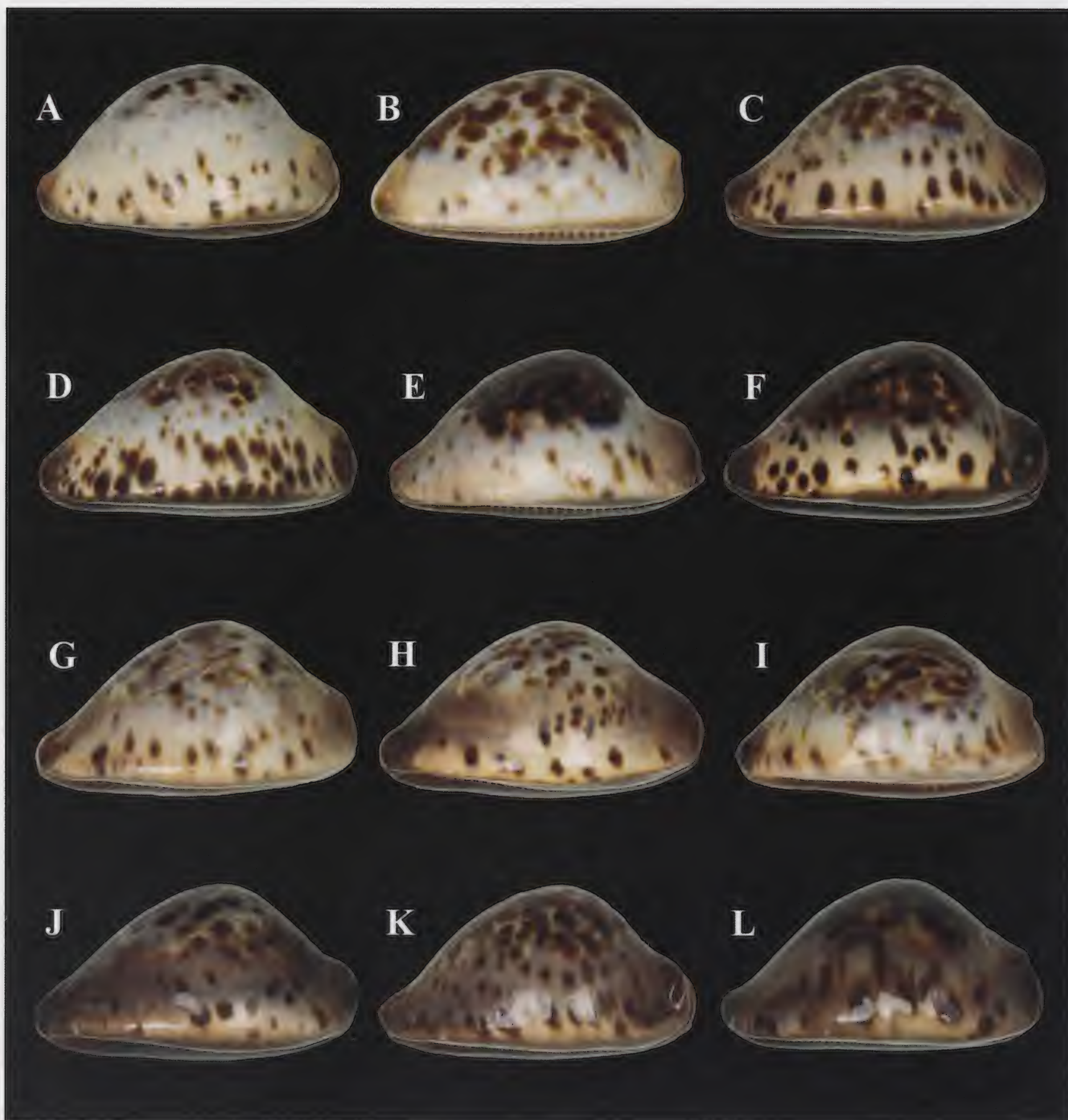


Plate 4. Left side views.



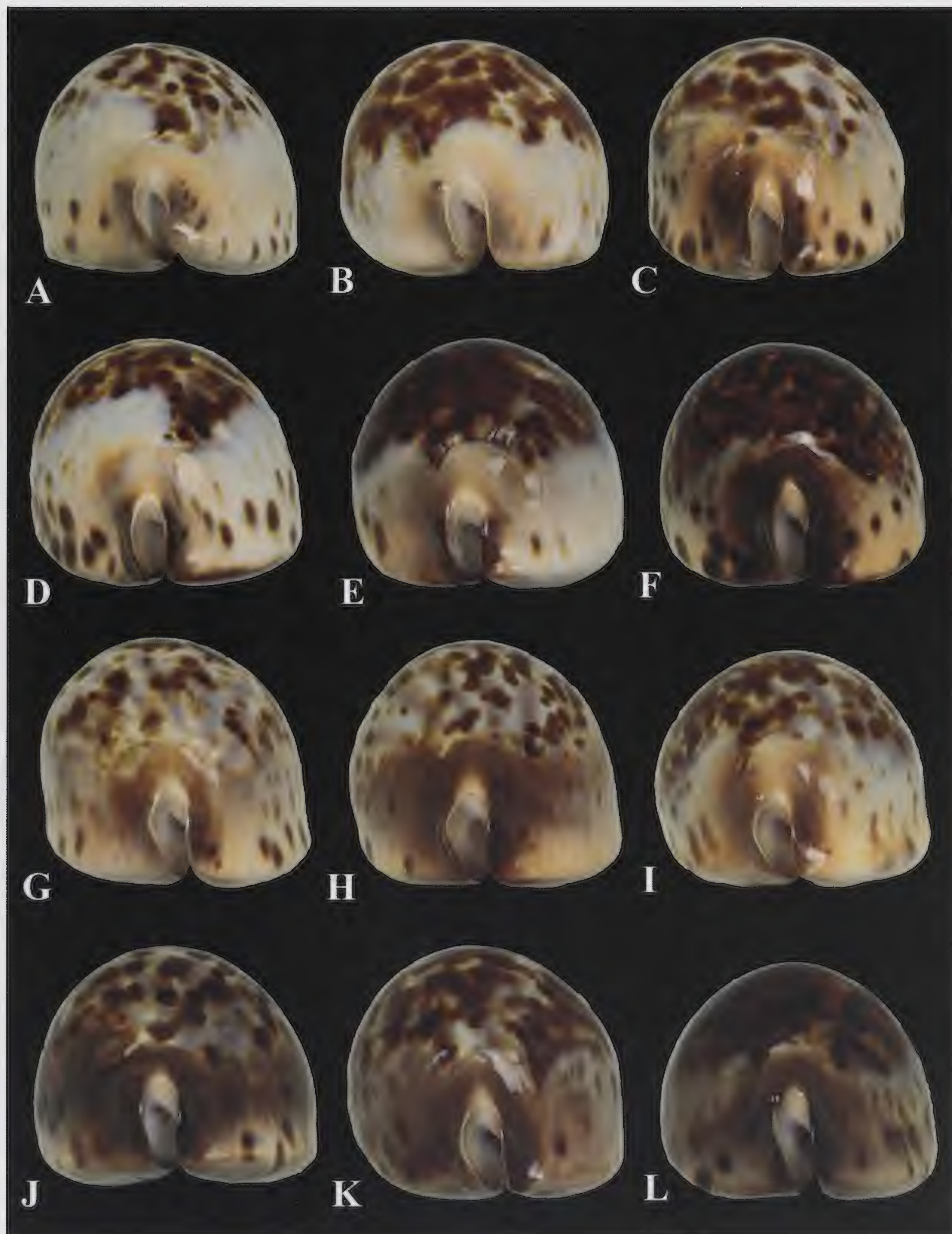


Plate 5. Posterior end views.



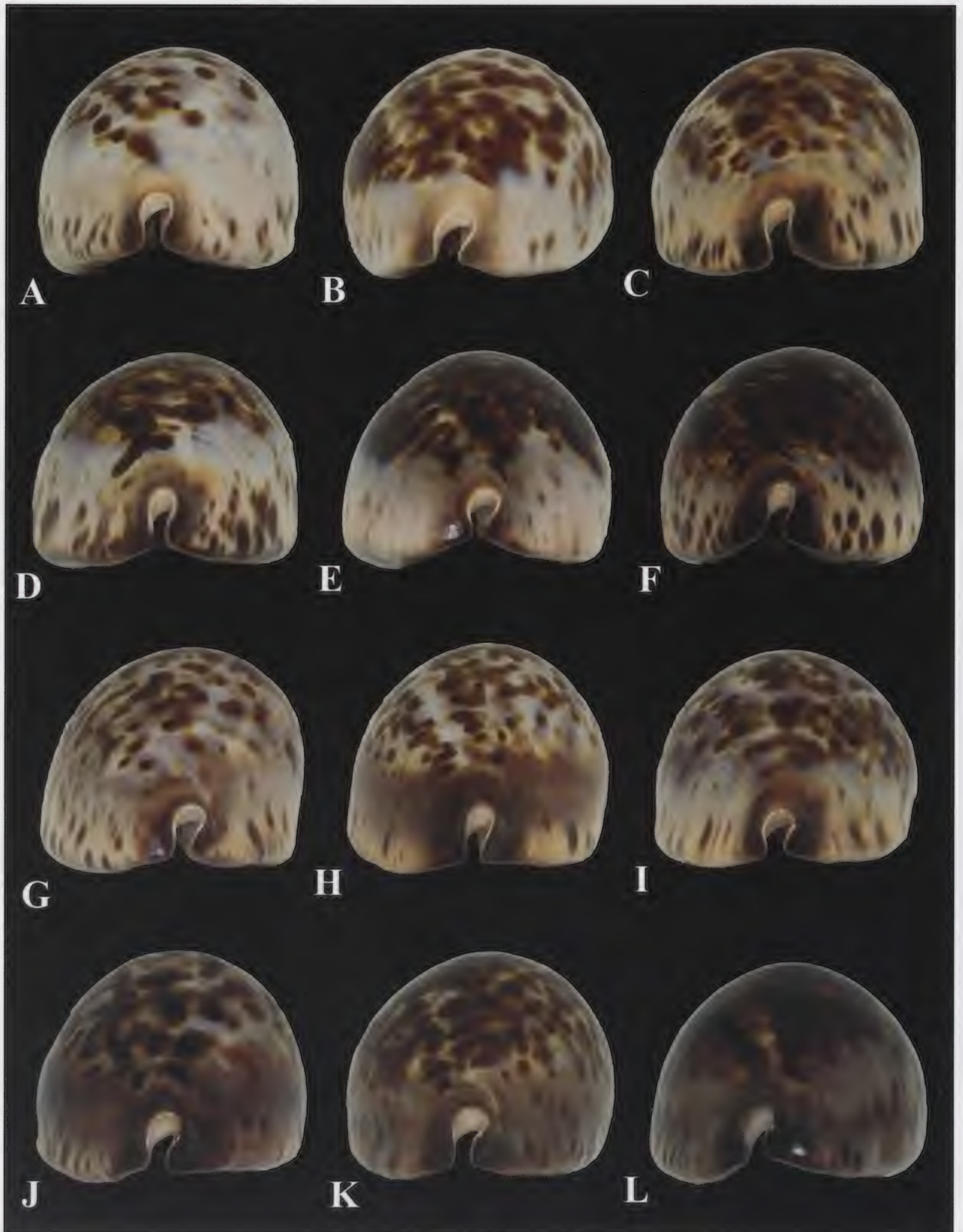
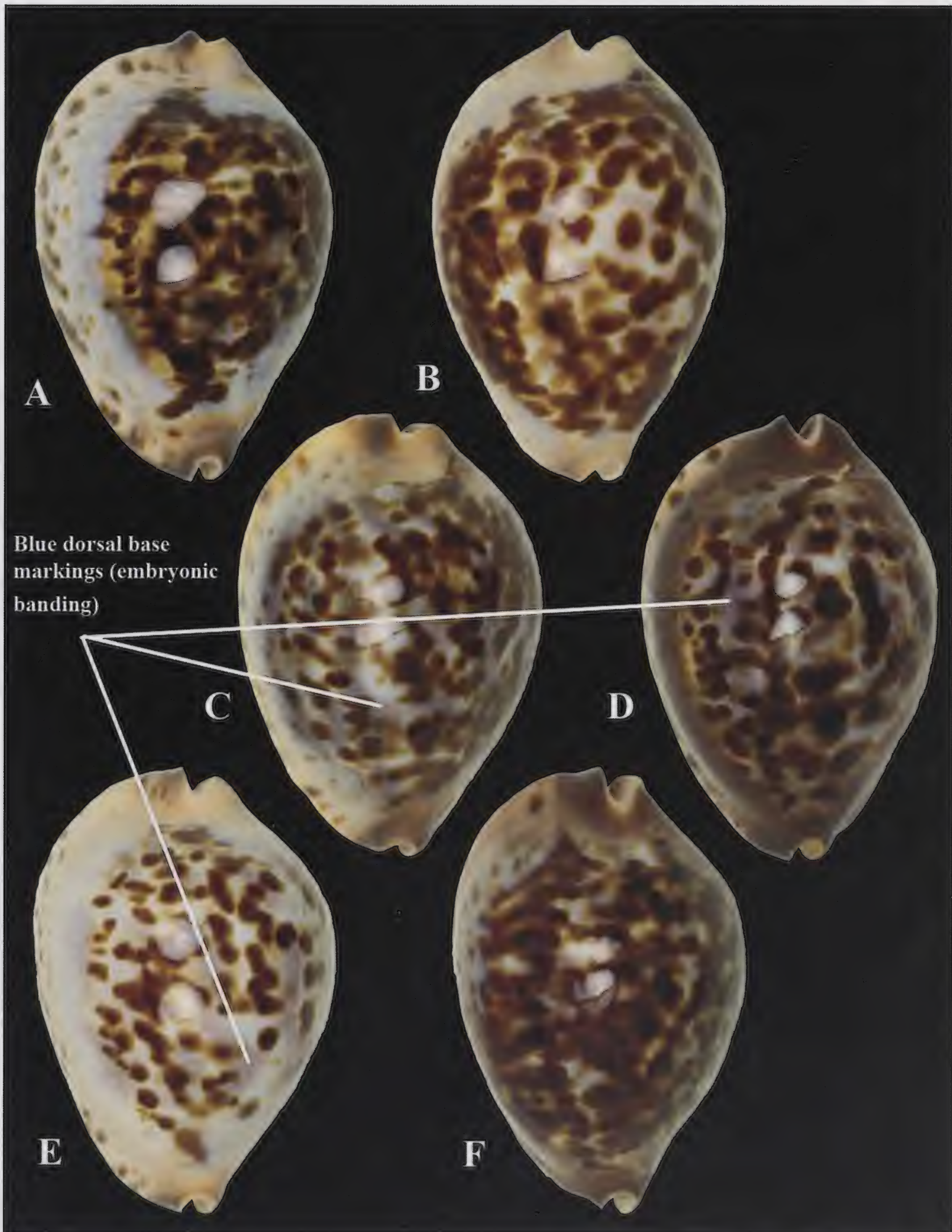


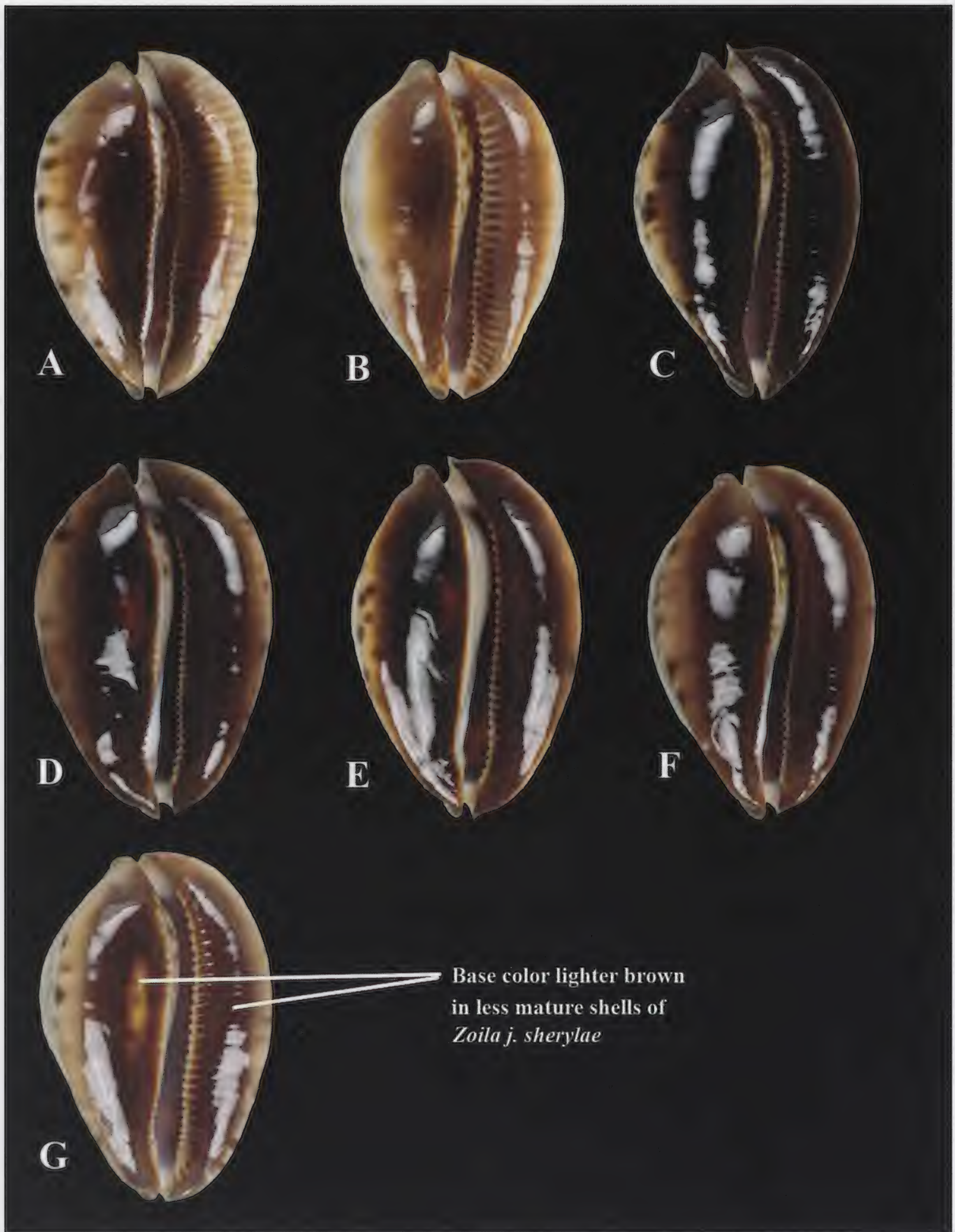
Plate 6. Anterior end views.





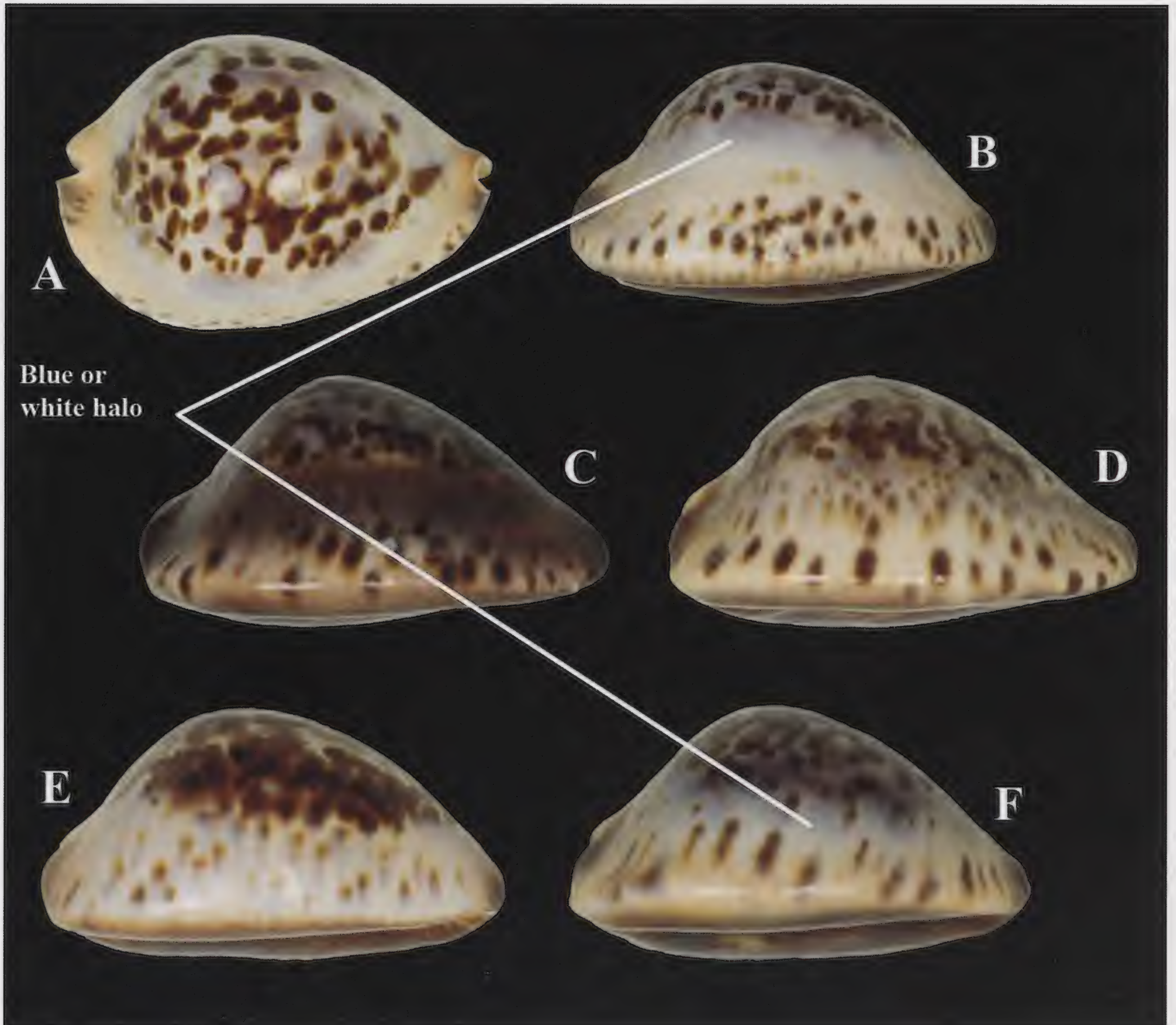
**Plate 7.** Compares the dorsal base color of *j. jeaniana* and *j. sherylae*. **A** = *j. jeaniana*, 74.3 mm (Plate 1D); **B** = *j. jeaniana*, 63.0 mm (Plate 1B); **C** = *j. sherylae*, 57.6 mm (Plate 1I); **D** = *j. sherylae*, 77.9 mm (Plate 1J); **E** = *j. jeaniana*, 75.8 mm (Plate 1A) and **F** = *j. sherylae*, 67.0 mm (Plate 1K). The blue dorsal banding (embryonic banding) can be seen in *J. sherylae* C and D just under the darker brown dorsal spotting. However, this character is not always visible through the darker dorsal markings as seen in *j. sherylae* F. Correspondingly, *j. jeaniana* can also show its embryonic banding as seen in *j. jeaniana* E.





**Plate 8.** Compares base color of *j. jeaniana* and *j. sherylae*. **A** = *j. jeaniana*, 75.8 mm (Plate 2A); **B** = *j. jeaniana*, 63.0 mm (Plate 2B); **C** = *j. jeaniana*, 66.1 mm (Plate 2F); **D** = *j. sherylae*, 77.9 mm (Plate 2 J); **E** = *j. sherylae*, 62.3 mm (Plate 2H); **F** = *j. sherylae*, 67.0 mm, (Plate 2K); and **G** = *j. sherylae*, 71.7 mm (Plate 2G). The dark base color characteristic of *j. sherylae* occurs in *j. jeaniana* as seen in image C. Correspondingly, lighter color bases can occur in less mature *j. sherylae* specimens as seen in G.





**Plate 9.** Compares the margin coloration of *j. jeaniana* and *j. sherylae*. **A** and **B** = *j. jeaniana*, 75.8 mm (Plate 1A); **C** = *j. sherylae*, 77.9 mm (Plate 3J); **D** = *j. sherylae*, 71.7 mm (Plate 3G); **E** = *j. jeaniana*, 63.0 mm (Plate 3B); and **F** = *j. sherylae*, 71.9 mm (Plate 3I). The blue or white halo characteristic of *j. jeaniana* can be difficult to observe as seen in E. Correspondingly, *j. sherylae* may have what appears to be a halo as seen in F.





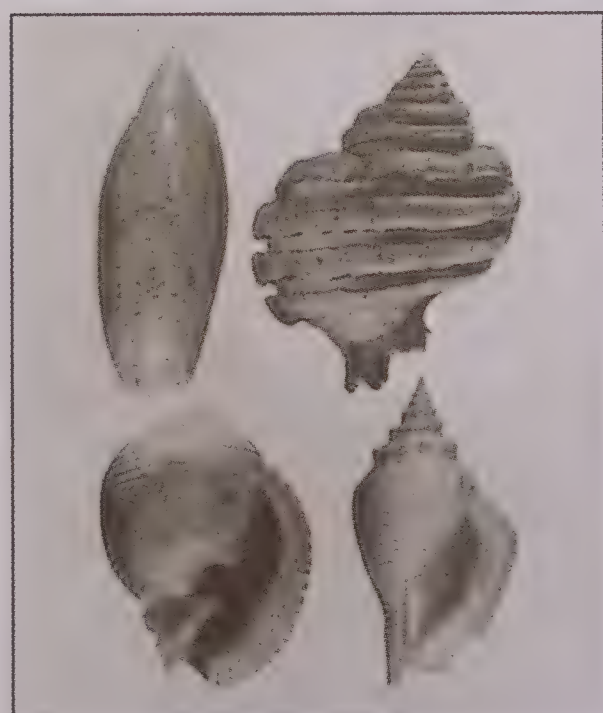
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*E. adansonianus adansonianus* (Crosse & Fischer, 1861), Bahamas, 106.1 mm. *B. poppei* (Anseeuw, 2003), Tonga Islands, 58.8 mm. *P. amabilis* f. *maurei* Harasewych & Askew, 1993, USA, 42 mm. *B. tangaroana* (Bouchet & Métivier, 1982), New Zealand, 55.9 mm. *P. quoyanus* (Fischer & Bernardi, 1856), Curaçao, 50.7 mm. *B. philpoppei* Poppe, Anseeuw & Goto, 2006, Philippines, 65.1 mm. *B. charlestonensis* Askew, 1987, Martinique, 77.3 mm. *B. midas* (Bayer, 1965), Bahamas, 82.7 mm.

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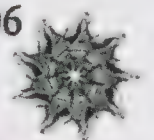
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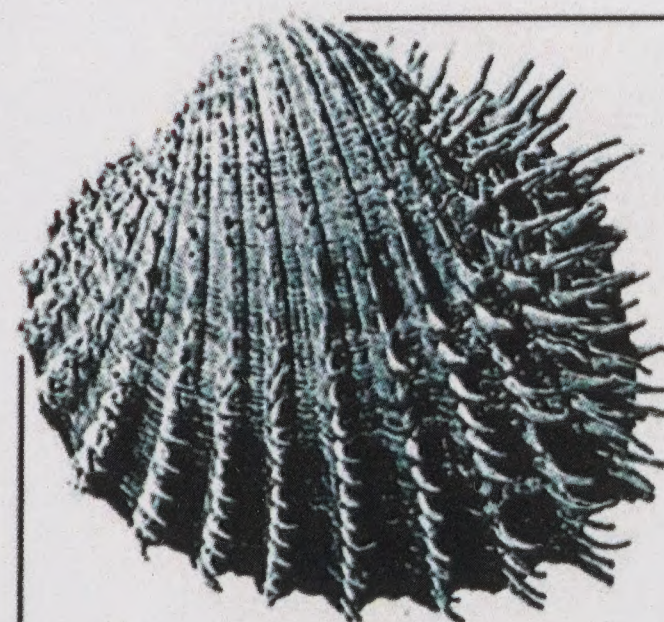
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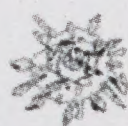


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**Back cover:** *Oniscidia dennisoni* (Reeve, 1842), length 53 mm, dredged at 90 m depth off Guajira Penninsula, Colombia; *Oniscidia lindae* (Petuch, 1987), length 36.8 mm, trawled at 120 m depth off Guajira Penninsula, Colombia; *Oniscidia matthewsi* (Emerson, 1967), length 29.4 mm, dredged at 40 m depth off Camocim, Ceará State, Brazil; *Morum oniscus* (Linnaeus, 1758), length 25 mm, in sand and coral rubble, 1 m depth off Cape Eleuthera, Eleuthera Island, Exuma Sound, Bahamas; *Morum strombiforme* (Reeve, 1842), length 28 mm, found fresh dead on the beach, Playa del Carmen, Quintana Roo State, eastern Yucatan Peninsula, Mexico; *Morum purpureum* Röding, 1798, length 24 mm, under coral rubble, 9-12 m, Curaçao; *Morum bayeri* Petuch, 2001, length 23 mm, in coralline algae, 3 m depth off Rio do Fogo, Rio Grande do Norte State, Brazil; *Morum berschaueri* Petuch and Myers, 2015, length 36 mm, dredged from 20 m depth in the Guarapari Channel, Guarapari, Espírito Santo State, Brazil; *Morum damasoi* Petuch and Berschauer, new species, holotype, length 17.5 mm, in coral rubble, 20 m depth off Coroa Vermelha, Abrolhos Platform, southern Bahia State, Brazil; *Morum mariaodeteae* Petuch and Berschauer, new species, holotype, length 18.5 mm, found in coralline algal rubble, 35 m depth off Camocim, Ceará State, Brazil. (Cover artistic credit: Rex Stilwill)



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